Behavioral changes, ecological niches and adaptive diversification in pigeons and doves

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Abstract

The extraordinary diversity of ecology, morphology, behavior, and species richness across the tree of life has long interested researchers. Understanding why and how lineages diversify in phenotype and species numbers remains, however, a major challenge in evolutionary biology because evolutionary diversification is a complex process influenced by a number of factors of diverse nature. The aim to this thesis is to obtain an integrated picture of the mechanisms that have led to the current biological diversity of pigeons and doves (order Columbiformes) by incorporating a crucial factor that has largely been neglected in evolutionary studies: the role of behavior. The general goal of the thesis is to show how changes in behavior can shape evolution by allowing individuals to modify the way they interact with their environment -their ecological niche. Such changes can modify the way selective pressures affect populations, thus favoring divergent selection that can promote adaptive diversification. The thesis addresses four main goals: the first is to describe the influence of behavioral changes in the adaptive diversification of a lineage (Chapter II). Second, I aim to show how the integration of such behavioral changes with geographical and ecological factors provides us with a better understanding of this process (Chapter III). Third, I describe a new method implemented to better study differences among the ecological niches of individuals and populations, which is necessary to link behavioural and evolutionary changes (Chapter IV). Finally, I use an experimental approach in feral pigeons (Columba livia) to understand the origin of existing ecological variation within populations, focusing on the role of increased competition and previous experience as main drivers of niche differentiation among individuals (Chapter V).

Resum

L'extraordinària diversitat de l'ecologia, morfologia, comportament, i la riquesa d'espècies en tot l'arbre de la vida ha interessat els investigadors des de fa molt de temps. No obstant, entendre com i per què els llinatges es diversifiquen en el seu fenotip i en nombre d'espècies segueix sent un repte important en biología evolutiva. La diversificació evolutiva és un procés complex, influit per múltiples factors de diferent naturalesa. L'objectiu d'aquesta tesi és obtenir una visió integrada dels mecanismes que han portat a la diversitat biològica actual del grup dels coloms (ordre Columbiformes) mitjançant la incorporació d'un factor clau que ha estat àmpliament ignorat en els estudis evolutius: el paper del comportament dels animals. L'objectiu fonamental de la tesi és mostrar com els canvis en el comportament poden donar forma a l'evolució permetent als individus modificar la forma en què interactuen amb el seu entorn -el seu nínxol ecològic-. Aquests canvis poden modificar la forma de les pressions de selección que afecten les poblacions animals, afavorint d'aquesta manera la selecció divergent que pot promoure la diversificació adaptativa. La tesi aborda quatre objectius principals: el primer és descriure la influència dels canvis de comportament en la diversificació d'adaptació d'un llinatge (Capítol II). En segon lloc, mostrar com la integració d'aquests canvis de comportament amb els factors geogràfics i ecològics ens proporciona una millor comprensió d'aquest procés (capítol III). En tercer lloc, descric un nou mètode implementat per millorar l'estudi de les diferències que poden existir en els nínxols ecològics dels individus i les poblacions, cosa que és nescessària per poder vincular els canvis de comportament amb canvis evolutius (capítol IV). Finalment, utilitzo una aproximació experimental utilitzant coloms roquers (Columba livia) com a organisme model per tal d'entendre l'origen de la variació ecològica existent dins de les poblacions. Aquest treball se centra en el paper de la competència entre individus i l'experiència prèvia en lús dels recursos com a principals motors de la diferenciació de nínxols entre els individus dins d'una població (capítol V).

Chapter 1

General Introduction

> *"Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends"* (R. 1842)*, referring to the group of finches that today bear his name).*

Researchers have long been fascinated by the extraordinary variety of life forms and have tried to understand how evolution generated all this diversity across the tree of life. Although great progress has been made in the last decades, understanding why and how lineages diversify in phenotype and species numbers remains a major challenge in evolutionary biology. The process of evolutionary diversification is complex, involving a variety of geographic and ecological factors as well as organism's features that can either facilitate or constraint evolutionary change. Consequently, there is not a single answer to understand why organisms diversify (Gavrilets & Losos 2009). However, important insight into the diversification process has been gained by the detailed analysis of particular well-studied lineages, as demonstrated by studies of Darwin finches from Galapagos, *Anolis* lizards from the Caribbean and Cichlid fishes from the African Great lakes.

In this thesis, I aimed to obtain an integrated picture of the mechanisms that have led to the current biological diversity of pigeons and doves (order Columbiformes). Like previous studies, I considered previous theoretical developments in addressing these mechanisms. Unlike previous studies, my research has paid particular attention on a crucial factor that has largely been neglected in evolutionary theory: the role of behavior. The main topic has been to argue that changes in behavior can shape evolution by allowing individuals to modify the way they interact with their environment (i.e. their ecological niche). Such changes can modify the way selective pressures affect populations, thus potentially favoring divergent selection that can promote adaptive diversification.

The thesis addresses four specific goals: First, I describe the influence of behavioral changes in the evolutionary diversification of Columbiformes (Chapter II). Second, I show how the integration of behavioral changes with geographical and ecological factors provides a better understanding of the process of adaptive diversification of the lineage (Chapter III). Third, I present a new method to better quantify differences among the ecological niches of individuals and populations, which is necessary to link behavioral and evolutionary changes (Chapter IV). Finally, I use an experimental approach in feral pigeons (*Columba livia*) to ask what make individuals change their behavior to exploit ecological opportunities, focusing on the role of increased competition and intrinsic resource preferences as main drivers of niche differentiation among individuals (Chapter V).

In the next section, I provide the necessary background to understand the results exposed in the thesis. With this aim, I have divided it into two main parts. In the first, I define a number of evolutionary concepts which are necessary to understand the process of biological diversification. I also describe the ecological niche concept, the difficulties associated with its definition, and its implications for the study of evolutionary ecology. Then, I focus on the explanations of whether and how changes in the ecological niche occur, and I review alternative theoretical backgrounds on the influence that behavioral changes might have in such process. Subsequently, I claim that incorporating the study of behavioral shifts is crucial for understanding evolution and I highlight that behavior should be investigated in the light of geographic and ecological factors that primarily influence the process of adaptive diversification. I end up by explaining why Columbiformes is an excellent group to investigate such questions.

In the second part of the Introduction, I focus on the causes of changes in behavior and describe why it is important to study intra-specific niche variation. I study the factors that could generate and maintain such variation, which represent the basis to understanding evolutionary dynamics. To understand why this is important, I highlight the need of conducting detailed experiments to disentangle the role of increased competition and resource preferences as main drivers of niche differentiation among individuals. Finally, I justify why I have used feral pigeons to study how intra-specific competition and intrinsic resource preferences variation might drive such differences.

A) The evolution of the ecological niche

1. Adaptation, speciation and diversification: different forms of evolution

To understand how species multiply and how phenotypic variation accumulates along the tree of life, we must define some of the key concepts in such processes. Below, I define several of such concepts that are necessary to understand both the patterns described and the processes inferred throughout this thesis.

The concept of evolutionary diversification refers to the changes that a lineage experiences over time in adaptive and non-adaptive phenotypic variation and/or species number (Schluter 2000). Adaptation into a variety of ecological niches is assumed to have generated most of the diversity across the tree of life (Darwin 1859; Simpson 1953; Schluter 2000). The idea that both the origin of new species and the evolution of ecological differences between them depends on ecological factors is referred to as the ecological theory of evolution (Schluter 2000). The theory, developed by Lack (1947), Dobzhansky (1951) and Simpson (1953) and updated by Schluter (2000), holds that both phenotypic divergence and speciation are ultimately the outcome of divergent natural selection stemming from differences in environments, resources, and resource competition (Schluter 2000).

The concept of "adaptation" is used for both a pattern and the process that leads to the pattern. Thus, an adaptation is any feature of organisms that has evolved via natural selection because it allows (or it allowed) individuals to better function in their current or past environment. Because by definition adaptations help organisms reproduce and survive in their environments, the ecological niche of animals is defined by behavioral, physiological and morphological adaptations (Hutchinson 1957). Behaviors, although generally considered highly flexible compared with other phenotypic traits, can also have a genetic basis and may evolve because they improve fitness. At the same time, the ability to modify behaviors can be itself an adaptation, for example when this depends on neural structures than enhance the cognitive functions associated with learning. As we will see later, this plasticity might have relevant evolutionary consequences.

Divergent selection occurs when natural selection pulls the phenotypes of individuals toward different directions as a consequence of contrasting environmental conditions. This can be promoted by dispersal events associated with range expansions (Ricklefs 2006), which provide novel ecological opportunities and create new selection pressures (Schluter 2001; Yoder et al. 2010). However, many populations have failed to diversify despite inhabiting environments potentially adequate for adaptive radiation (Seehausen 2006). Why should this happen? Below, I expose that the existence of new ecological opportunities is not enough to promote diversification. Rather, animals must modify their behavior to take advantage of such new opportunities.

2. The ecological niche

Organisms are not distributed randomly in ecosystems. Rather, they occupy different ecological niches, defined by the conditions that they tolerate and the resources they are able exploit. Understanding how organisms' ecological niches change is crucial to understand many ecological processes, like the distribution and abundance of species. Since the emergence of the ecological theory of evolution, the niche concept has also become central to understand the process of evolutionary diversification. Ecological niches are compromised by constraints that impede their evolution (e.g. niche conservation associated with morphological and/or physiological specializations), and the forces promoting their change through natural selection or learnt behaviors (Wiens & Graham 2005). The relative importance of both forces represents a continuum that describes differences between organisms in their capacity to modify their niche. For example, specialist species that have evolved to exploit a narrow range of resources are expected to show more inertia to change their niche than generalist species that exploit wider ranges of resources. If follows that to fully understand how ecology affects evolution, we need to see the current niche of species as the result of current and past environmental conditions and constraints. In this thesis, I study the ecological niche by integrating retrospective historical analyses and experimental studies regarding changes in the niche at the species- and individual-level.

Defining the ecological niche is not straightforward, however. The term was coined by Joseph Grinnell (1917), who defined it as the habitat features that determine the species'a bility to persist and produce descendants. For example, Red Crossbills (*Loxia curvirostra*) inhabit coniferous forests, where they feed in high branches foraging on the seeds they remove from pines with the help of their specialized beak. Also, they fly around the forest in search of mature pines and escape from predators by hiding among branches. This definition refers to a property of the environment rather than of the species and is seen as an available place in the community (Schoener 1989).

The concept of the niche was reformulated later by Elton (reviewed in Elton 2001) to explain the functional role that a species or individual plays in the ecological community, rather than being based on its requirements to survive and reproduce. Following the previous example, Red Crossbills niche may be defined as a pine predator that plays a function as a seed disperser and sometimes may become a food resource for forest raptors.

Finally, George Hutchinson (1957) introduced an integrative definition of niche focused on the properties that enable different species to persist there. Hutchinson proposed that the ecological niche is a “hypervolume” in multidimensional ecological space, determined by a species’ requirements to reproduce and survive (Hutchinson 1957). Each dimension in the niche space represents an environmental variable relevant for an organism’s persistence. A crucial point here is that these variables can be both abiotic and biotic (for example, the range of temperatures where an organism can live but also more complex measurements as resource availability or degree of inter-specific competition). This differs from former views in that ecological niches are dynamic: the presence of one species may limit the presence of another through interspecific competition, modifying the position of species’ niches within the multidimensional space. Repeating the example of Red Crossbills, their presence does not only depend on an adequate range of temperatures or the presence of conifers, but also will depend on the year’s pine production (they might move if production is very low) or also they might be displaced by competitive species (e.g. squirrels).

Therefore, Hutchinson's definition includes both the ecological requirements of a species and its functional role in the local community.

Hutchinson described the fundamental niche of a species as the full range of biotic and abiotic environmental conditions where it could survive and reproduce (Hutchinson 1957). In contrast, the realized niche is the subset of such conditions where the species actually can persist given the presence of other species competing for the same resources (Hutchinson 1957). Red crossbills could potentially live in all coniferous forests with pines (fundamental niche) but are excluded from the areas where the abundance of squirrels is so high that they outcompete for the pines, narrowing their realized niche. This idea is relevant to understand key elements of this thesis. First, one of its main implications is that it paves the way for the idea that different populations of the same species may occupy different ecological niches if environmental conditions differ. Second, this idea can –and should- be even expanded to the individual level: individuals within populations may vary in a number of ecological dimensions (e.g. the resources they use). From an ecological and evolutionary point of view, the species-level concept of ecological niche is indeed useful for comparative approaches, but intraspecific variation in the ecological niche should be further considered in niche research. For example, some Red Crossbill individuals might change their habits and start to exploit pines that are so small that are not consumed by squirrels and this may allow those individuals to survive and reproduce more than other conspecifics (increase their fitness). Despite having potential implications for population dynamics and evolution, this idea has been largely neglected in niche theory and only recently started to be seriously considered (reviewed in (Bolnick et al. 2003; Araújo et al. 2011).

2.1. The difficulty of describing the ecological niche of organisms

Although Hutchinson's formalization is potentially and theoretically useful to understand how organisms interact with their environment, in practice the number of niche dimensions is potentially infinite and this makes the niche difficult to describe properly (see in De Cáceres et al. (2011). As a result, it may happen that, when studying the niches of different species, a niche overlap among species may be the consequence of not having measured certain niche axes that might segregate these species ecologically. Thus, one of the main difficulties is to identify those ecological axes that are crucial to define an organism's realized niche. However, this may sometimes be possible. For example, (MacArthur 1958) showed niche segregation in five species of warblers along only three niche axes (nesting time, foraging mode and foraging height). Thus, only by determining relevant ecological niche axes we will be able to study the ecological and evolutionary consequences of modifications in the ecological niche. In Chapters II and III, I identify relevant axes of variation in the ecological niches of pigeons and doves and use recently developed phylogenetic comparative methods to describe how changes in these axes have shaped their evolutionary diversification.

2.2. Niche changes: ecological opportunities and Innovation

As stated above, the ecological niche of an organism is the result of the interaction with conspecifics, with other organisms and with their physical environment. Because in animals these interactions are mediated by behavior, the ecological niche cannot be understood without including the behavioral decisions they take, which determine how to choose mates, reproduce, care for their young, find and defend resources and avoid predators. Because behavior is plastic by definition, behavioral shifts could be seen as major drivers of changes in the ecological niche of animals. However, this is not always the case because animals tend to select the habitats and resources to which they are best suited.

Two elements facilitate that animals modify any of the dimensions of their ecological niche. First, novel ecological opportunities (i.e. the existence of resource types under-utilized by other taxa) must be available. This often means "being in the right place at the right time" (Schluter 2000), and can arise in two ways. First, new opportunities may arise as a consequence of a change in the biotic or abiotic environment. For example, the extinction of competing species may allow other species to exploit resources that were previously not available. Classic examples include the replacement of the non-avian dinosaurs by mammals at the end of the Cretaceous or the fast diversification of cichlid fish after the formation of isolated lakes in the African rift valley (Seehausen 2006). The alternative is that animals encounter new opportunities when they colonize new areas (Price 2008) where the exploitation of such new resources allows them to survive and reproduce.

Second, changes in the niche often require the appearance of a new trait (also referred to as key innovations) that allows the exploitation of niches that cannot be efficiently exploited without the trait. The difference here is that newly exploited resources might have been there all the time, but only when the innovation appeared was the organism able to exploit it. An example might be the acquired capacity to fly by birds and mammals, which opened the door for new niches to be exploited. In this thesis I focus on a different kind of innovation that might as well promote niche shifts: behavioral innovation. Indeed, changes in behavior are necessary to take advantage of new ecological opportunities (Lefebvre et al. 1997, 2004).

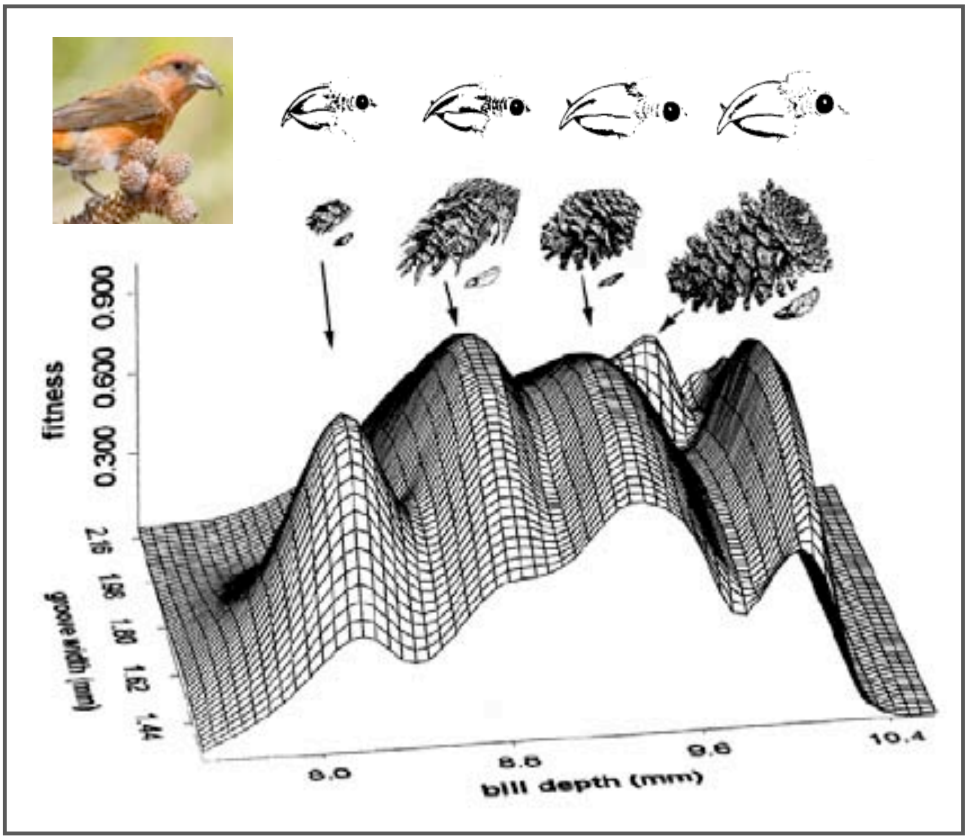
2.3. Behavioral changes as neglected drivers of adaptive diversification: or "rejecting the unidirectional arrow"

The idea that a behavioral change can lead populations to evolve phenotypes that differ from those of their ancestors –evolution towards new adaptive optima- is simple. A change in the way an animal interacts with its environment may allow it to alter its niche or invade a novel ecological niche. In such "new" niche, novel selective pressures may act on the individual and its descendants. Such new selective forces may be divergent in that they favor phenotypes that differ from that of their ancestors. For example, a different beak shape might allow a bird to better exploit a new resource. This can be visualized following the example of Red crossbills. In a now classic paper, Benkman (2003) suggested that divergent selection associated with the use of different resources caused adaptive diversification. Thus, in five different closely related species of the Red crossbill complex, natural selection adjusted beak shape of individuals to better exploit different types of pines (Figure 1). Following this example, in a scenario where some individuals within a population change their behavior (behavioral innovation) and start exploiting a new type of pine (ecological opportunity), we can hypothesize that natural selection will rapidly select those phenotypes most suited to open these new pines. In a number of generations, if the direction of selection remains stable, this might lead the population towards a new beak shape optimum. The process by which a behavioral shift spurs evolutionary change is known as the “behavioral drive” (Wyles et al. 1983).

The “behavioral drive” hypothesis thus argues that behavior can act as a driver of evolutionary diversification by changing the way individuals interact with their environment, placing divergent selection pressures on populations (Wcislo 1989; Robinson & Dukas 1999; Huey et al. 2003; Price 2008; Duckworth 2008). This can bring evolutionary modifications in three different ways. First, natural selection may pull the population’s phenotype towards a new adaptive optimum (i.e. the phenotypic state in which an individual gets maximum benefits from resources). Second, if the new environmental challenges may be dealt with in different ways, a higher disparity among species under the new selective regime will be promoted (Collar et al. 2011). Finally, the new behavior can be fixed if selection favors morphological and physiological adjustments to exploit the new niche, a phenomenon known as genetic assimilation (Price 2008).

However, the role of behavior in evolution has generally been under-appreciated. The traditional view has long been that animals are passive agents of selection. Thus, adaptation is a process by which natural selection shapes organisms to fit preexisting environmental scenarios. In words of Kevin Laland, “the causal arrow points in one direction only” where the sources of selection –environments- shape the traits of organisms (Laland et al. 2000). Although the idea that behavior can affect evolution is not new (Baldwin 1896), it is increasingly recognized that animals are not passive agents of selection, but rather they can alter selective pressures by changing their behavior (Wyles et al. 1983; West-Eberhard 1989; Robinson & Dukas 1999; Huey et al. 2003; Duckworth 2008). Thus, it is more realistic to think that there is a dynamic feedback where organisms drive environmental changes and the environments that have been modified by these organisms subsequently select them with traits suited to deal with such environment. This is the idea behind the concept of “niche construction”, which holds that organisms can and do modify their own and/or other’s niches through their metabolism, activities and choices (Odling-Smee, F.J., Laland, K.N. & Feldman 2003). The defining characteristic of niche construction is not the modification of the environment per se, but rather the change in the organism’s niche (Laland et al. 2000). These changes may include dispersal, migration and habitat selection, where organisms relocate in space to modify the environments they experience. Such “behavioral niche construction” is expected to be crucial for organisms’ chances to survive and reproduce, but its ability to lead new ecological pressures that entail subsequent changes in morphology has been largely neglected in the study of evolutionary diversification.

Figure 1: Modified from Benkman (2003). Adaptive peaks for beak morphology (depth) for red crossbill species based on their foraging performance as a fitness surrogate.



One of the reasons why behavioral traits have usually not been considered in evolutionary studies is that, being considered labile, their possible role is not predicted to be detectable along the evolutionary history of a lineage. However, some behavioral traits can be considerably constant through evolutionary time. For example, a frugivorous animal may potentially shift to incorporate hard seeds in its diet. However, the costs of developing a digestive system that allows a fine process of such resources may be too costly and thus the foraging behavior, although apparently labile, may not change along the evolutionary history of a lineage. A recurrent theme of the present thesis is to show that these types of behavioral shifts have been crucial in the adaptive diversification of animals. In other words, I claim for the reconsideration of causality in ecological and evolutionary studies: the "causal arrow" should be considered to be bidirectional (see Laland et al. (2000).

2.4. Behavioral shifts may also inhibit evolution: the Bogert effect

While behavioral changes may promote evolutionary change, they also might retard evolutionary change (Bogert 1949). Plastic changes in behavior are an important way through which animals respond to new ecological pressures (Sih et al. 2011). Such plastic behavioral changes are at the forefront of the response of animals to new selective pressures, which may hide genetic variation from natural selection, and hence inhibit evolutionary change. This is known as the "Bogert effect" (reviewed in Robinson & Dukas (1999); Huey et al (2003) and Price et al (2003)).

Whether behavior facilitates or inhibits evolution must be resolved on empirical grounds. However, current evidence about whether behavior generally favors or inhibits evolutionary diversification is scanty and contradictory. A few studies have shown that bird lineages with larger brains, a surrogate for their higher propensity for behavioral changes, have diversified more extensively both taxonomically and morphologically (Nicolakakis et al. 2003; Sol et al. 2005; Sol & Price 2008). However, Lynch (1990) found no evidence that post-cranial morphological evolution has been faster in mammalian lineages with larger brains). This hypothesis is explicitly addressed in Chapter II. In this work, I used a comparative phylogenetic retrospective approach for the study of the evolution of pigeons and doves. I apply, for the first time, recently developed evolutionary models to show that key changes in behavior were associated with changes in the evolutionary trajectory of functionally-relevant phenotypic traits, and that the rate of such changes was also accelerated when such changes occurred.

3. Integrating biogeography, ecology and behavior to study lineages' adaptive diversification

Unlike behavior, the roles of geographical and ecological factors in determining species diversification are well supported. For example, dispersal events associated with range expansions are known to limit gene flow, facilitating reproductive isolation (Ricklefs 2006; Price 2008). This is particularly true when the invaded region offers new ecological opportunities and contains environments that differ in some extent to the ancestral ones. Thus, the combined effect of biogeographic and ecological factors appears essential in promoting evolutionary diversification (Darwin 1859; Simpson 1953; Schluter 2001). The rapid diversification of Darwin finches is a well-known example. Geographic isolation was promoted by the existence of multiple islands and adaptive diversification derived from the availability of a variety of ecological opportunities that required different phenotypic features to be efficiently exploited (Lack 1947; Grant & Grant 2008). However, such well-known examples are rare in the literature, and behavior is not generally considered together with geographic and ecological factor in driving evolutionary diversification. In Chapter III, I integrate the relative roles of geographical, ecological and behavioral factors to understand Columbiformes' diversification. I argue that extrinsic factors may have set the stage for evolutionary diversification, but cannot explain the deterministic pattern of morphological variation we see across species of pigeons and doves (Todd Streelman & Danley 2003). The use of novel phylogenetic methods allows me to confirm the importance of behavioral changes in the process, but also to show that such changes are contingent on geographic and ecological factors, which pave the way for behavioral changes.

4. Why Columbiformes? The ecological niche of pigeons and doves

One of the difficulties of studying the evolution of the ecological niche is that it is generally difficult to define and quantify. However, a suitable approach is trying to identify the crucial axes of variation that define how organisms are adapted to their environments. Although such approach will always be incomplete, it may be possible to identify such axes of variation in some groups. Pigeons and doves are one such group. Their ecological niche can be described by several axes of variation. First, one macro-ecological feature, habitat type, divides species in those inhabiting open or forested areas. Second, two micro-ecological ones regarding the foraging niche (foraging strategy and the food type) are also important (Gibbs, D., Barnes, E., Cox, J. 2001). Almost all species can be divided into having a terrestrial or an arboreal foraging mode and foraging in fruit or hard seeds and grain ((Gibbs, D., Barnes, E., Cox, J. 2001); Figure 2). Arboreal species primarily forage on fruits found on the trees and rarely descend to the ground while terrestrial species forage in the ground where species foraging on seeds and grain may be differentiated from those foraging on fruit. Finally, a geographic axis may also be important in their evolutionary history: more than half of the species inhabit islands, which potentially allow us to investigate the role of geographic isolation in speciation and diversification. Pigeons and doves have widely colonized most of the world including five continents and extremely isolated islands, facilitated by their high dispersal ability (Pereira et al. 2007), are represented by a large number of species (> 300), and show an important variation in their morphology (e.g. three orders of magnitude in body mass), making them a suitable group to study the process of ecological diversification.

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B) Causes of behavioral shifts and within-population niche variation

Assembling evidence that behavior drives evolution is important to understand evolution. However, this is half of the story. What we also need to understand is: why should a group of individuals sharing a common environment diverge in the use of food resources? This question has recently attracted great interest among evolutionary ecologists (Araújo et al. 2011) because of its implications to determine ecological interactions, population dynamics and evolutionary dynamics of organisms (Bolnick et al. 2007, 2011; Araújo et al. 2011; Dall et al. 2012).

1. Why is there divergence in resource use?

Two main explanations have been put forward to explain why animals differ in resource use (Svanback & Bolnick 2005). The "competition" hypothesis assumes that individuals share preferences for resources and that resource limitation drives conspecific competitors to minimize resource use overlap (Svanback & Bolnick 2007). Ecologists have particularly predicted resource competition to be one of the main drivers of intraspecific differences in resource use (Van Valen 1965; Bolnick et al. 2003; Svanback & Bolnick 2005; Tim Tinker et al. 2012). Within-population niche variation increases when food becomes scarce or monopolized by competitors (Roughgarden 1972; Svanback & Bolnick 2005, 2007; Bolnick et al. 2010; Tim Tinker et al. 2012) and a number of recent observational and experimental works have confirmed that competition enhances individual niche variation (Svanback & Bolnick 2005, 2007; Araújo et al. 2008; Pires et al. 2011; Tim Tinker et al. 2012; Laskowski & Bell 2013).

Alternatively, it is possible that changes in the ecological niche of animals do not only depend on environmental factors, but also on intrinsic traits of individuals that make them to differ in resource preferences. Variation in resource preferences can be the consequence of morphological, physiological and/or behavioral trade-offs where, for example, individuals that are more efficient in exploiting certain resources might not be good at exploiting alternative resources due to limitations on morphology (e.g.

body size) physiology (e.g. ability to digest different resources) or behavior (e.g. increased performance to exploit different resources acquired through learning).

The two hypotheses are not mutually exclusive and may interact with each other to constitute the among-individual variation existent within many animal populations (Bolnick et al. 2003; Araújo et al. 2011). For example, under increased competition conditions, it could be that only the most plastic animals are able to successfully manage to get the necessary amount of food to survive and reproduce. The theoretical idea that the interaction among these intrinsic and extrinsic factors could determine individual variation in resource use has wide ecological and evolutionary implications, because it might determine which individuals are able to successfully deal with challenges such as the current human-induced rapid environmental changes, thus paving the way for changes in evolutionary changes (Sol et al. 2013; Sih 2013).

2. *Methodological considerations*

Despite the notorious increased interest in within-population variation, current evidence of the role of different factors in determining why should animals vary in their resource use –and why some might vary while others do not- is hindered by a number of methodological limitations (Araújo et al. 2011; Dall et al. 2012). To adequately address this question, it is critical to have accurate measures of both resource preferences and resource use, to test the consistency in such preferences over time, to examine the existence of trade-offs in resource efficiency and their underlying causes, and to monitor changes in resource use under different environmental scenarios (e.g. with and without competition). Moreover, the costs of such changes need to be quantified and the influence of previous experience needs to be ruled out. To our knowledge, such an integrative approach of the factors behind individual difference in the niche has not been addressed before. In Chapter V, I use an experimental approach using wild-captured and captive-bred feral pigeons from two different populations to address this question. I apply the recently implemented method described in Chapter IV (Cáceres et al. 2011) to show that competition promotes increased variation and specialization among individuals sharing a common environment, but I also provide evidence that such variation depends on intrinsic individual traits and on the ability of individuals to respond plastically to varying environmental conditions.

3. Why feral pigeons (Columba livia)?

Feral pigeons are adequate organisms for studying the causes and consequences of resource partition for a number of reasons. (Giraldeau & Lefebvre 1985) showed that individuals from the same group foraging on a mixed food patch showed striking differences in resource use. Also, several studies regarding food choice found individual differences in foraging preferences (Shettleworth 1985; Killeen et al. 1993; Plowright & Redmond 1996; Plowright & Landry 2000) that have been suggested to be particularly important when animals have been food deprived (Killeen et al. 1993). Inman et al. (1988) provided one of the first evidences that plastic responses to increased competition can lead feral pigeon individuals to modify their resource use facilitate partitioning. Moreover, although group-foraging species, like feral pigeons, are predicted to be more positively benefitted from resource partition, no studies have examined the consistency of such partition through time, which is crucial in determining differences in ecological interactions and population dynamics. Finally, resource partition in groups of animals taking profit from human-derived resources is interesting for two reasons: urban populations usually face decreased levels of inter-specific competition, which is predicted by theory to facilitate resource expansion (Van Valen 1965); and we do not know if urban species that partition resources have more chances to successfully deal with human-induced rapid environmental changes. Indeed, such ability for resource partitioning within a species may provide pigeons with the ability to exploit a given mixed patch faster than other species with narrower-ranged foraging widths, outcompeting them.

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Chapter 2

Behavioural changes and the adaptive diversification of pigeons and doves [1, 2]

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[1] With Daniel Sol, Salvador Carranza and Jeremy Beaulieu. **Proceedings of the Royal Society B (Cover image)**; 22 March 2013 vol. 280 no. 175520122893

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Abstract

What factors determine the extent of evolutionary diversification remains a major question in evolutionary biology. Behavioural changes have long been suggested to be a major driver of phenotypic diversification by exposing animals to new selective pressures. Nevertheless, the role of behaviour in evolution remains controversial because behavioural changes can also retard evolutionary change by hiding genetic variation from selection. In the present study, we apply recently implemented Ornstein-Uhlenbeck evolutionary models to show that behavioural changes led to associated evolutionary responses in functionally relevant morphological traits of pigeons and doves (Columbiformes). Specifically, changes from terrestrial to arboreal foraging behaviour reconstructed in a set of phylogenies brought associated shorter tarsi and longer tails, consistent with functional predictions. Interestingly, the transition to arboreality accelerated the rates of evolutionary divergence, leading to an increased morphological specialization that seems to have subsequently constrained reversals to terrestrial foraging. Altogether, our results support the view that behaviour may drive evolutionary diversification but they also highlight that its evolutionary consequences largely depend on the limits imposed by the functional demands of the adaptive zone.

Key words: evolutionary rates, behavioural drive, Bogert effect, Columbiformes, evolutionary diversification, Ornstein-Uhlenbeck

Much of current diversity across the tree of life is thought to have arisen from divergent selection leading to adaptation into a variety of ecological niches [1–3]. Thus, the extent of adaptive diversification is widely held to be enhanced by ecological opportunities [4,5], either associated with environmental changes or dispersal events that extended geographical ranges [6]. However, there are numerous situations where populations have failed to diversify despite inhabiting environments apparently conducive to adaptive radiation [7]. These situations highlight that divergent selection is not solely a function of the environment, but also depends on the way organisms interact with it [8,9]. Because changes in behaviour are necessary to take advantage of new ecological opportunities [10,11], behaviour has long been suggested to be a major driver of evolution in animals [9,12–24]. Mayr [15, p. 604], for example, wrote: "A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behaviour. The other adaptations to the niche, particularly the structural ones, are acquired secondarily". More than 50 years after Mayr's quote, however, whether and how behaviours influence evolution are still the subject of intense debate [9].

Behaviour can act as a driver of evolutionary diversification by changing the way individuals interact with their environment, thereby placing divergent selection pressures on populations that promote adaptive divergence [9,19,22–24]. As suggested by Collar and colleagues [25], when there is a change in the way individuals interact with the environment, subsequent evolutionary changes can be promoted in two different ways. First, natural selection may pull the population's phenotype towards a new adaptive optimum. Second, if the new environmental challenges may be dealt with in different ways, the rates of phenotypic disparity within the new selective regime may also increase [25]. Although both mechanisms may act simultaneously to increase diversification, their consequences for the tree of life are different. The first mechanism results in an increased phenotypic disparity within the clade as a whole, but not among species experiencing the same selective regime. By contrast, the second mechanism predicts a higher disparity among species under the new selective regime [25].

While behaviour is classically viewed as an important driver of evolutionary change, the possibility that behaviour can sometimes also act to retard evolution has also been acknowledged [13,26,27]. On one hand, plastic changes in behaviour are an important way through which animals respond to new ecological pressures [28], which may hide genetic variation from natural selection and hence inhibit evolutionary change (the so-called Bogert effect; reviewed in [22,23,26]). While some studies suggest that behavioural changes do not necessarily prevent natural selection from operating on other characters when individuals are exposed to new ecological pressures [27], this does not rule out the possibility that the Bogert effect plays a major role in retarding adaptive evolution on an evolutionary time scale, contributing to patterns of evolutionary stasis and niche conservatism. On the other hand, if a behavioural change brings the population close to an adaptive peak that is functionally demanding, stabilizing selection will impose strong limits to subsequent phenotypic diversification and hence favour evolutionary stasis and niche conservatism.

Current evidence about whether behaviour generally favours or inhibits evolutionary diversification is insufficient to draw firm conclusions. A few comparative studies in birds have revealed that lineages with a higher propensity for behavioural changes, as reflected by their larger brains, have generally experienced more extensive evolutionary diversifications in body size [29], subspecies richness [30], and species richness [31]. Nevertheless, it should be noted that behaviour may favour evolutionary change by mechanisms other than exposing animals to divergent selective pressures, such as by facilitating the establishment in a novel region or by reducing extinction risk [15,24,32–34]. In addition, Lynch [35] found no evidence that post-cranial morphological evolution has been faster in mammalian lineages with larger brains.

A more direct approach to study whether changes in behaviour drive or inhibit evolution would be to assess whether past behavioural changes can explain current patterns of phenotypic diversification. Recent progress in phylogenetic comparative methods provides a framework for such a retrospective approach [36–39]. With a well-supported phylogeny and information on contemporary phenotypic variation, it is possible to study the evolutionary trajectory of a phenotypic trait after a change in behaviour by fitting different evolutionary models of phenotypic evolution. The hypothesis that behavioural changes can retard phenotypic changes may be described with an Ornstein–Uhlenbeck (OU) model under stabilizing selection where phenotypic variation oscillates around a common phenotypic optimum for all species irrespective of their behavioural state. The alternative possibility, that behavioural shifts create novel selection pressures that lead to adaptations towards different phenotypic optima, can be approximated by fitting an OU process with a different optima for each selective regime [36,37]. Using OU models, a few studies have yielded evidence of divergence towards different morphological optima associated with behavioural changes in foraging strategy [40], habitat use [25,41] and locomotive strategy [42]. However, in-depth biological interpretations of these associations between behavioural shifts and evolutionary change under an OU process have been hindered by the restrictive assumption that both the strength of selection towards the new optima and its rate of stochastic variation away from the optima do not vary among selective regimes [43]. Recent OU model implementations, however, now allow for the separate estimation of selective forces pulling species to different phenotypic optima and the range of variation around these optima [43]. This new framework allows researchers to move forward towards more mechanistic questions on the nature of the evolutionary consequences of changes in the selective regimes (e.g. do behavioural shifts accelerate or limit evolutionary change?).

In the present study, we use the aforementioned flexible OU model to investigate the consequences of changes in foraging behaviour in the morphological diversification of pigeons and doves (order Columbiformes). Columbiformes experienced a worldwide radiation from the Early Eocene, presumably facilitated by their high dispersal ability [44], which allowed them to diversify into a large number of species (> 310) and colonize an extremely diverse range of habitats in all continents except Antarctica [45]. During their geographic expansion, pigeons and doves probably encountered a myriad of different environments [45], which may have required behavioural adjustments that may or may not have led to subsequent evolutionary adjustments. Our focus here is on transitions from terrestrial to arboreal behaviour and vice-versa, which represent a fundamental divergence in the way pigeons and doves exploit the resources. Almost all members of the lineage can be easily classified as either terrestrial or arboreal in their foraging behaviour, with only a few species combining both behaviours [45]. Tree-dwelling Columbiformes inhabit forested habitats and feed on fruit they obtain by perching on tree branches whereas terrestrial-foraging species occur in both forested and open habitats and primarily feed on seeds and grains, but also fruit [45].

With the aim of investigating whether and how such behavioural changes may have influenced morphological diversification, we built a molecular phylogeny of the Columbiformes encompassing over half of the extant species. Using this phylogeny as a framework, we reconstructed changes between arboreal, terrestrial, and generalist foraging behaviours and used these changes as the basis for fitting a variety of OU models to describe subsequent morphological evolution while taking into account uncertainties in phylogeny and ancestral state reconstructions. The OU models were contrasted with Brownian motion (BM) models, which assume that phenotypic variation accumulates at random over time without a defined trajectory [38,39]. As different morphological traits may follow different evolutionary trajectories under similar ecological scenarios, we used a variety of morphological traits predicted to have functional consequences for pigeons' foraging performance and integrated them in a few multivariate axes explaining the vast majority of variation in morphology. However, we predict that the evolutionary consequences of changes in foraging behaviour should be primarily reflected in the hindlimb and the tail. This is because shorter hindlimbs and a longer tail are expected to increase stability in birds perching on slender and unstable branches by keeping the centre of mass close to the perch whereas a long hindlimb increases stride length and hence enhances speed during terrestrial locomotion [46,47]

Methods

Taxon sampling and phylogenetic analyses

We constructed our phylogenetic hypothesis for Columbiformes using both Maximum Likelihood (ML) and Bayesian methods using six mitochondrial and three nuclear genes (see Appendix A1 in the supplementary material for the detailed information regarding the construction of the phylogenies) from the GenBank database. We obtained enough information for 156 species of pigeons and doves (about half of the whole order) plus eight outgroups to root the tree. A list of all the specimens included in the phylogenetic analyses with the GenBank accession numbers can be found in the supplementary material (Appendix A2). The alignment is available from TreeBASE (study ID 13646).

Foraging behaviour

We obtained information on each species' biology from published literature sources, mainly from Gibbs et al [45]. We considered as terrestrial those species that primarily obtain their food (usually seeds and grain, but also fruits) by searching on the ground and as arboreal those that primarily forage on fruits found on trees and rarely descend to the ground. Almost all species could be easily classified to have either a terrestrial or arboreal foraging mode (see Table A4). However, 12 species with a mixed strategy (i.e. those species regularly using both foraging modes) were classified into an intermediate category (i.e. generalists). A simplified alternative analysis with species classified into only two main foraging categories (i.e. terrestrial and arboreal) yielded similar results.

Ancestral state reconstructions

To reconstruct the history of foraging behaviour in Columbiformes, we used stochastic character mapping [48,49]. This is a Bayesian method that, given a phylogeny and discrete character states for extant species, applies MCMC to sample the posterior probability distribution of ancestral states and timings of transitions on phylogenetic branches under a Markov process of evolution [48,49]. The R package *phytools* [50] was used to build stochastic character mapped reconstructions for each of the 500 trees sampled from the posterior distribution of the BEAST. The resulting 500 reconstructions of behavioural states and phylogeny represent a set of phylogenetic topologies, branch lengths, and habitat histories sampled in proportion to their posterior probabilities. All these trees were used in subsequent analyses as a way for integrating over uncertainty in phylogeny and ancestral states.

Morphology

Information on five ecologically-relevant morphological characters (length of the tarsus, tail, wing, beak, and body mass) was obtained for the 156 species from the literature [45,51](Table A4). Although the size of the hindlimb was described with a single trait (the length of the tarsus), previous work has shown that the tarsus length is correlated with the length of the other hindlimb bones across flying animal groups (R^2 of 0.68 and 0.85 with femur and tibia lengths, respectively; [52]. For twelve species we could not find information on body mass, and these were estimated with imputation techniques based on multiple regressions [53].

Morphological evolution may be tightly correlated with changes in overall body size, and this allometric relationship can lead to equivocal positive results if the function of the character is confounded with that of body size. To tackle this difficulty, we conducted a phylogenetic size correction following Revell [54] to obtain morphological measurements independent from body size (body mass, in our case). All measurements were log-transformed and body mass was in addition first cubic root transformed. The procedure uses the residuals from a log-log least squares regression analysis, while controlling for non-independence due to phylogenetic history. Once these corrected scores were obtained, we conducted a phylogenetic PCA analysis again following Revell [54]. The resulting PCA scores for each axis were used as the input to investigate the most likely evolutionary scenarios of morphological evolution. As phylogenetic principal components provide estimates of the eigenstructure with lower variance relative to non-phylogenetic procedures when residual error is autocorrelated among species, this should reduce type I error when they are used in subsequent analyses [54].

To illustrate the amount of unique morphospace occupied by each foraging behaviour category we used a bivariate plot of the first two components from the phylogenetically-corrected principal components analysis. This plot shows a projection of the tree into morphospace (phylomorphospace plot) in which lines connect hypothetical ancestral phenotypes to the known or estimated phenotypes of their descendants (i.e. a representation of the phylogenetic morphospace [50]).

We also obtained similar information for 150 additional species not present in the phylogeny to test whether our subset of 156 species accurately represent the morphospace of the entire clade. With these additional data, we confirmed that the species sampled in the study were not a biased sample of the complete Columbiformes order (Table A5). We quantified the disparity of the raw values of all morphological traits by computing the average-squared Euclidean distance among all pairs of points within the dataset using the “disp.calc” function in the *GEIGER* package written for R [55]. This allowed us to investigate if disparity differs across lineages showing diverging foraging behaviours, and whether it is different between different morphological traits that may be under different selective regimes.

Model selection for morphological evolution

We fit five different OU models of character evolution to morphological data to test whether behavioural changes have been associated with selective constraints on the evolution of several morphological trait axes. The simplest model was an OU model with a single optimum (θ) applied to all branches regardless of the behavioural state ("OU1" model). The remaining four OU models differed in how the rate parameters were allowed to vary in the model. The first was an OU model with different phenotypic optima means (θ_x) and both identical strengths of selection (α_x) and rate of stochastic motion around the optima (σ^2_x) acting on all selective regimes ("OUM" model). This model is equivalent to that implemented by Butler and King [37]. We also fit a model that only allowed strengths of selection to vary among selective regimes (α_1, $\alpha_{2\ \ldots}$; "OUMA" model) as well as one that only allowed of rates of stochastic evolution away from the optimum to vary (σ^2_A, $\sigma^2_{B\ldots}$; "OUMV" model). Finally, we fit a model that allowed all three parameters (theta, alpha, sigma) to vary among different selective regimes ("OUMVA" model). All models were fit using the R package *OUwie* [43]. We used a model averaging approach where we calculated the Akaike weights for each model (i.e. the relative likelihood of each model) by means of the second-order Akaike information criteria (AICc), which includes a correction for reduced sample sizes [56]. The parameter estimates for each model were then averaged together, using their corresponding Akaike weight as the weights.

An alternative possibility would be that morphology varies at random following a Brownian motion process (BM), where phenotypic variation accumulates with time. Although Brownian motion does not necessarily represent a model of random variation (it can be also consistent, for example, with neutral genetic drift, selection towards a moving optimum, or drift-mutation balance [43]), rejecting this as the best model implies that phenotypic evolution has not followed a random evolutionary trajectory. We also tested the possibility that the BM process has a different rate of evolution among different selective regimes (terrestrial, generalist, arboreal, BMS model).

Finally, we estimated the phylogenetic half-life ($t_{1/2} = \ln(2) / \alpha$) for each PC axis in each selective regime. This parameter is defined as the time required for the expected phenotype, starting in an ancestral state and evolving under a new selective regime, to traverse half the morphological distance from the ancestral state to the optimum [36], and was estimated in relative time units for comparative purposes among selective regimes only.

Results

Phylogenetic analyses

The results of the ML and Bayesian analyses were congruent (Figs. 1, B1), and corroborate the main phylogenetic relationships among Columbiformes found in a previous analysis by Pereira et al. [44]. The main difference is that in our ML and Bayesian trees the clade B (*sensu* Pereira et al. [44]) is considered sister to clades A and C instead of being sister to only clade C. However, in both the present analysis and Pereira et al [44], the bootstrap support and posterior probabilities for the relationships among clades A, B, and C is low (see Fig. B1 of the present manuscript, and Figs. 1 and 2 from [44]).

Character reconstructions and evolutionary transitions

Figure 1 shows one of the 500 sampled trees from the stochastic character mapping reconstruction of changes in foraging behaviour derived from the ultrametric Bayesian analysis in BEAST. Two species for which no morphological information was available (*Raphus cucullatus* and *Pezophaps solitaria*) were pruned from the trees.

Table A6 in the supplementary material indicates the mean, median, SD, modal number, maximum and minimum number of transitions estimated for each sampled tree from/to all foraging strategies. The modal number of transitions computed from the sample of 500 trees was 20. According to the reconstructions, terrestrial pigeons and doves were inferred to have changed their foraging behaviour twelve times (seven to generalist and five to arboreal foraging). The modal number of transitions from generalist lineages was eight (six times to arboreal and twice to terrestrial foraging). Finally, arboreal lineages did not show any transition to other foraging strategies (modal number = 0 for both transitions to terrestrial and generalist foraging strategies) suggesting that specialization in arboreal foraging may be an evolutionary dead-end (Fig. 1; see also Appendix A7 in the supplementary material for a formal analyses of evolutionary transitions rates with BayesTraits).

Defining the morphospace

To investigate whether behavioural changes have led to morphological changes, we started by defining the morphospace of Columbiformes with a size-corrected phylogenetic PCA. We restricted our analyses to the first three axes, which together accounted for 90.79 % of the morphological variation of the lineage (Table A8). The first axis correlated mostly with the length of the tail and less strongly with tarsus length; the second axis primarily correlated positively with tarsus length and negatively with tail length. Finally, the third axis correlated with both wing length and beak length.

The morphospace defined by the PC axes showed that terrestrial species occupy a broader space than arboreal and generalist lineages, which instead showed a more clumped phenotypic distribution pattern (Fig. 2; see also Figs. C1 and C2 in the supplementary online material). This result was further confirmed when comparing morphological disparity metrics, which were higher for terrestrial species than for arboreal and generalist species for all morphological traits (Table A5). The extent of increased morphological diversity in terrestrial lineages was particularly pronounced in the case of tarsus length, for which disparity in terrestrial species was more than three times higher than in arboreal-dwelling species. The phylogenetic morphospace representation showed that a significant part of the variation in PC1 corresponded to the effect of a single phylogenetic clade (i.e. species in the bottom right morphospace representation correspond to clade B, defined above), which could affect the interpretation of the model results. This pattern of phylogenetic clustering was not found neither for PC2 (Figure 2) nor for PC3 (Figures C1 and C2).

Evolutionary model fitting

All BM models received less support than any of the OU models for all PC axes and body size evolution (Table 1), suggesting that the evolution of these traits oscillates at least in part around one or more phenotypic optima. In the OU models, the estimated optima were found within the values realized for extant species in all cases (Table 2), suggesting that the models were a realistic description of current morphological patterns.

There was substantial support for the OUMVA model of evolution (AICw ranging from 0.612 to 0.699 respectively; Table 1) for PC1, PC2 and body size, and with the exception of OU1 for PC1, all alternative models received low support (AICw < 0.09). Indeed, the model averaged parameter estimates from all five OU models suggest that the adaptive optima differed among behavioural strategies (see mean phenotypic optimum scores in Table 2), although both phenotypic optima were much more similar between arboreal and generalist lineages, compared to terrestrial-dwelling lineages. Tail length was the morphological trait most strongly loading in PC1 whereas tarsus length was the trait most strongly loading in PC2. Taken together, the values of phenotypic optima suggest that species evolved towards shorter tarsi and longer tails when changing from terrestrial to either arboreal or generalist behaviour (Table 2). The evolution of PC3 (described mainly by wing length and secondarily by beak length) was best fit by an OUMA model although alternative models, such as OU1, also received some statistical support (Table 1). It should be noted, however, that differences between the phenotypic optima of each selective regime were comparatively much smaller for PC3 than those inferred for both PC1 and PC2 (Table 2), consistent with its lower functional relevance in the context of foraging substrate. Finally, although the optimum for body mass was estimated to be larger for arboreal and generalist lineages (Table 2), this could simply be the consequence of the pulling effect of some very small terrestrial-dwelling Neotropical species belonging to clade B (sensu Pereira et al. [44]; see Fig 1).

Interestingly, we found striking differences in the parameters describing the evolution of morphological traits between different selective regimes. Although individual estimates varied considerably from tree to tree, the strength of selection (α) towards the phenotypic optimum was consistently higher in PC1, PC2, and body mass, and consistently lower in PC3, after a change towards arboreal or generalist foraging strategy than when the lineage used a terrestrial strategy (see Table 2). Similarly, the rate of stochastic motion away from the optimum (σ^2) was consistently higher in terrestrial lineages than in the other two strategies, despite a range of estimates across our tree set (Table 2). Finally, phylogenetic half-life for either PC1, PC2 or body size is markedly lower in arboreal and generalist lineages (Table A9). In particular, the phylogenetic half-time estimated for body size is about four times faster when governed by either the arboreal or generalist selective regimes (Table A9).

Discussion

Evolutionary models always represent an over-simplification of the evolutionary processes that have shaped adaptive diversification within a lineage, as incorporating all factors that may affect evolutionary change is virtually impossible [57]. At present, however, the implementation of models that allow for both the strength of selection and the rate of stochastic motion around the phenotypic optima to vary between presumed selective regimes [43] makes it possible to fit more mechanistic evolutionary models. The success of such a model selection approach is nonetheless contingent on the existence of a robust phylogenetic hypothesis and of several independent behavioural transitions that allow the assessment of convergent evolution for lineages under similar selective regimes (e.g. all lineages that adopted an arboreal foraging behaviour). When these conditions are met, as they are here, the comparison of different models may provide important insights into the factors influencing evolutionary diversification [25,40–42,58–62].

Our results shed new light on the unresolved controversy of whether behavioural shifts accelerate or inhibit evolutionary change [23,26]. First, we find that past changes in foraging behaviour of Columbiformes have brought associated changes in functionally relevant morphological traits in the direction predicted by eco-morphological theory. Second, by applying recently implemented evolutionary models, we provide evidence that changes in the way Columbiformes obtain their foraging resources are associated with accelerated rates of evolutionary change in some morphological characters. Nevertheless, the results also highlight scenarios where a behavioural change may limit subsequent evolutionary diversification. Thus, the functional demands of arboreality seem to limit further diversification of arboreal-dwelling lineages, perhaps representing a form of evolutionary dead-end.

Our analyses suggest that the evolutionary trajectories of morphological traits have changed in a predictable manner associated with a change in foraging behaviour, mostly in the PCAs related to tail length (PC1, but also PC2) and hindlimb (PC2) morphology as well as overall body size, but not for the evolution of wing and beak lengths (PC3). The best evolutionary models for PC1, PC2 and body size were multiple-peak OU models, with a divergent optimum for terrestrial specialists compared to both generalists and arboreal specialists. With the exception of body size, where functional implications of different optima are unclear, the existence of different phenotypic optima is in agreement with biomechanical predictions [47,63–65]. Long hindlimbs are thought to increase stride length and enhance speed in terrestrial locomotion whereas short hindlimbs and longer tails should increase stability in birds perching on slender and unstable branches by keeping the centre of mass close to the perch [47]. Our results fit well these expectations, with changes to arboreal behaviour associated with evolutionary trajectories towards shorter tarsi and longer tails, and changes to terrestrial behaviour leading to opposed trajectories. While with a retrospective analysis it is not possible to demonstrate that behaviour is the driving force behind morphological evolution, the stronger support for OU models relative to BM models is incompatible with a scenario where morphological evolution occurs at random with a correlated effect on behaviour. Moreover, although morphology can influence behavioural decisions, for example by affecting motor performance in different substrates, the existence of stabilizing selection pulling lineages with different foraging behaviours towards different phenotypic optimum zones is difficult to understand unless each foraging behavioural type imposes a different selective regime.

However, behavioural changes not only can promote phenotypic evolution by imposing selection towards different adaptive peaks, but also by facilitating the use of available resources in different ways within a selective regime [25]. By investigating the variation in the strength of selection (α) and the stochastic motion (σ^2) parameters [43], we show that terrestrial lineages indeed exhibited a more relaxed effect of stabilizing selection and a higher rate of stochastic variation in the size of the tarsus, tail and body than the other lineages, which may explain their higher morphological disparity. On the contrary, foraging on trees may require higher levels of morphological specialization, as shown by the reduced variation in the morphospace, which may subsequently limit the performance of individuals in other foraging contexts. This may explain why transitions from arboreal foraging behaviour to any of the other behavioural strategies have rarely occurred in the evolutionary history of Columbiformes. Thus, it may very well be that a change in behaviour increases phenotypic disparity within the clade as a whole and, at the same time, either increases or reduces rates of evolutionary diversification within the clade depending on the intensity of stabilizing selection.

Although the factors that have triggered changes in foraging behaviour in Columbiformes are unknown, there are two obvious possibilities. The first is the colonization of areas where the distribution of resources forces individuals to change their behavioural strategy [57]. Dispersal ability is held to be one of the most important factors related to diversification in birds [24,66], and may have also played a major role in the evolutionary history of Columbiformes. Pereira et al. [44] identified at least fifteen independent intercontinental colonization events along the evolutionary history of Columbiformes, apart from many colonization events of remote islands. It is quite conceivable that the high dispersal ability of pigeons and doves [44,45] may have contributed to the adaptive diversification of the group by facilitating the colonization of distant regions offering novel ecological opportunities. Moreover, the reproductive isolation and small population numbers associated with allopatric (and peripatric) events of colonization may have facilitated rapid evolutionary shifts in isolated populations of Columbiformes. The second factor that may have triggered changes in foraging behaviour in Columbiformes is competition [4], which may also be related (although not necessarily) to the invasion of remote areas. On the West Indian island of Barbados, for example, Zenaida doves (*Zenaida aurita*) aggressively defend feeding territories from conspecifics, but in some areas individuals have recently started feeding in large unaggressive groups with conspecifics. This behavioural shift, facilitated by the availability of a novel resource opportunity, has been suggested to be the consequence of competition for territories, which forced less competitive individuals to use alternative resources [67]. The finding that body size notably varies among closely related arboreal species could indeed be a consequence of competition if, as suggested by Diamond [68,69], differences in body size allows coexistence among species that consume fruits of different sizes in branches of different diameters.

Once a novel behaviour has established in the population, evolution may proceed remarkably rapidly [24]. Our results estimate that substantial changes in morphology can occur in short periods of time, particularly after a behavioural change to arboreality. Such relatively short periods needed to produce important divergence in morphological traits contrast with the long evolutionary period since Columbiformes diverged from their ancestor (between 83 and 107 Mya, as estimated by Pereira et al. [44]), and agrees with empirical evidence that changes in locomotive demands may exert strong selection on pigeons' morphology [46]. Thus, our study adds to the extensive comparative and experimental evidence supporting the importance of locomotion in the evolutionary diversification of animals, as exemplified in the classical adaptive radiation of *Anolis* lizards (reviewed in [57], and see also [70]).

Overall, our results support the widely held yet rarely tested hypothesis that modifications in behaviour can promote adaptive diversification of a whole clade by exposing individuals under different selective regimes to divergent selective pressures. At the same time, the results also highlight that changes in behaviour may either increase or reduce rates of evolutionary diversification within each selective regime depending on the force of stabilizing selection. Coupled with other mechanisms, such as a high dispersal ability and competition, behaviour may thus be a powerful force in the evolutionary diversification of animals. To better integrate behaviour into the ecological theory of evolution, however, we need further studies specifically examining the interplay between colonization, competition, and behavioural shifts in determining the adoption of novel ecological opportunities and subsequent phenotypic divergence. These studies are likely to provide important insight into the causes underlying the enormous adaptive diversification experienced by some lineages.

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Table captions:

Table 1: Average AIC weights (AICw) representing the relative likelihood of each of the seven evolutionary models investigated to morphological data for PC1, PC2, and PC3 axes and body size computed after fitting all evolutionary models on 500 reconstructions of the foraging strategy obtained from the trees after stochastic character mapping

	BM1	BMS	OU1	OUM	OUMV	OUMA	OUMVA
PC1	<0.001	<0.001	0.255	0.035	0.012	0.060	0.638
PC2	<0.001	<0.001	<0.001	0.019	0.313	0.009	0.612
PC3	<0.001	0.002	0.322	0.130	0.085	0.388	0.073
body size	0.061	0.017	0.045	0.057	0.088	0.034	0.699

Table 2: Model averaged parameters for every PC axis and body mass. The means and both 2.5% and 97.5% quantiles around the average (in parentheses) are shown for each selective regime for the mean phenotypic optimum (θ), the strength of selection (α), and the rate of stochastic motion (σ^2). The proportion of trees where mean adaptive optima or parameter estimates significantly differ between terrestrial and arboreal/generalist selective regimes is indicated in all cases

	terrestrial	generalist	arboreal	
	$\theta1$	$\theta2$	$\theta3$	Prop $\theta1 \neq \theta2, \theta3$
PC1	-0.05 (-0.09 / 0.01)	-0.14 (-0.26 / -0.07)	-0.13 (-0.26 / -0.07)	98.9% (>)
PC2	0.19 (0.16 / 0.23)	-0.10 (-0.25 / 0.04)	-0.10 (-0.25 / 0.04)	99.7% (>)
PC3	0.03 (0.02 / 0.05)	0.02 (-0.03 / 0.10)	0.01 (-0.03 / 0.08)	80% (>)
body size	1.66 (1.60 / 1.81)	1.88 (1.71 / 2.00)	1.85 (1.69 / 2.00)	97.1% (<)
	$\alpha1$	$\alpha2$	$\alpha3$	Prop $\alpha1 \neq \alpha2, \alpha3$
PC1	8.86 (2.06 / 15.13)	20.9 (3.26 / 43.6)	21.4 (3.27 / 48.0)	98.8% (<)
PC2	7.16 (1.83 / 10.2)	13.4 (3.68 / 34.1)	14.7 (6.19 / 35.2)	94.1% (<)
PC3	19.6 (11.6 / 27.9)	16.2 (10.8 / 23.9)	17.4 (11.0 / 25.6)	90.9% (>)
body size	3.79 (<0.01 / 9.68)	16.0 (1.06 / 61.3)	15.0 (0.99 / 60.5)	96.3% (<)
	$\sigma^2 1$	$\sigma^2 2$	$\sigma^2 3$	Prop $\sigma^2 1 \neq \sigma^2 2, \sigma^2 3$
PC1	2.66 (0.79 / 4.83)	0.99 (0.02 / 2.42)	1.14 (0.04 / 2.31)	99.2% (>)
PC2	1.82 (1.42 / 2.25)	1.36 (0.11 / 3.44)	1.02 (0.06 / 3.27)	81.9% (>)
PC3	0.86 (0.53 / 1.21)	0.81 (0.48 / 1.17)	0.81 (0.49 / 1.17)	76.3% (>)
body size	0.90 (0.52 / 1.51)	0.37 (<0.01 / 0.93)	0.45 (<0.01 / 0.91)	98.3% (>)

Figure 1. Sample tree of one of the 500 foraging behaviour reconstructions generated through stochastic character mapping. Coloured branches illustrate foraging behaviour estimated at each branch: terrestrial lineages (in blue), generalist (in red) and arboreal (in green). Changes may occur within branches because reconstructions depict not only the states at nodes but also the states at all points along a branch between nodes.

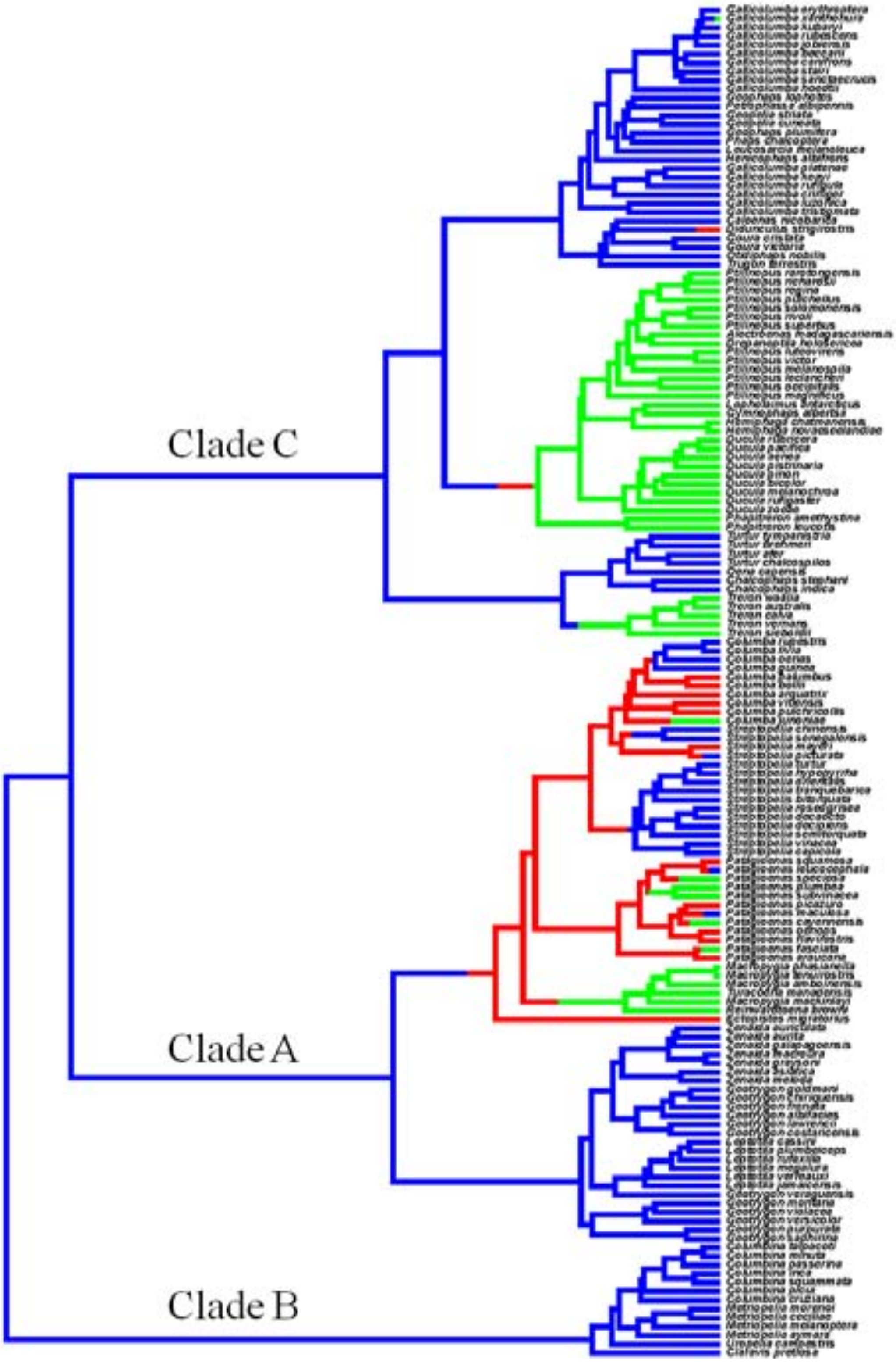
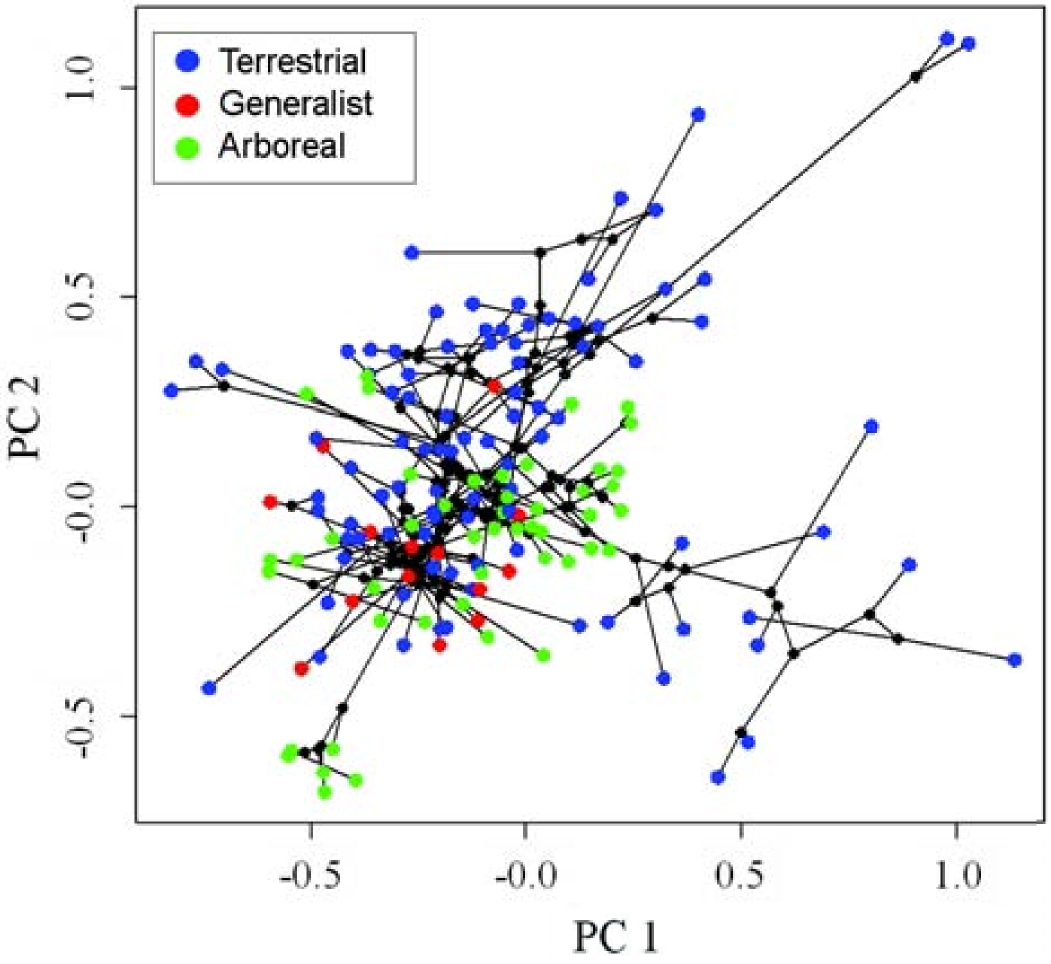


Figure 2. A phylogenetic morphospace representation of all 154 Columbiformes that superimposes the branching patterns of the phylogeny (black lines) on the plot of the two first PC axes from the phylogenetic PCA. Species are coloured with respect to their foraging behaviour category: terrestrial (blue), generalist (red) and arboreal (green).



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Appendix S1: Taxon sampling and phylogenetic analyses

To construct our phylogenetic hypothesis for Columbiformes, we searched for sequences of mitochondrial and nuclear genes in the GenBank. We obtained enough information for 156 species of Columbiformes (about half of the whole order) plus eight species of the genera *Anhima, Caprimulgus, Chaetura, Crax, Gallus, Hirundapus, Podargus* and *Struthio* to root the tree. A list of all the specimens included in the phylogenetic analyses with the GenBank accession numbers can be found in the supplementary material (Table A1). The genes used included six mitochondrial genes: small ribosomal subunit (12S rRNA), cytochrome b (cytb), NADH dehydrogenase subunit 2 (ND2), ATP synthase F0 subunits 8 and 6 (ATPase8/6), part of the cytochrome c oxidase subunit III (CO3), cytochrome c oxidase subunit I (CO1); and three nuclear genes: β fibrinogen intron 7 (FIB7); recombination activating protein (RAG-1); and the interphotoreceptor retinoid-binding protein (IRBP). Information on the length of the genes, percentage of missing data, and variability of the sequences and models of sequence evolution applied to each partition is presented in the supplementary material (Table A2). We aligned DNA sequences using MAFFT v.6 [1] with the options maxiterate 1000 and localpair. We eliminated poorly aligned positions using G-blocks [73] with low stringency options [74].

We performed phylogenetic analyses using Maximum Likelihood (ML) and Bayesian methods. We additionally performed separate ML analyses on all nine independent partitions (12S, cytb, ND2, ATPase8/6, CO3, CO1, FIB7, RAG-1, and IRBP) to test for conflicting signal among genes (data not shown). We selected best-fitting nucleotide substitution models for each partition under the Akaike information criterion [75] using jModelTest v.0.1.1 [5]. We estimated the GTR+I+G model independently for the 12S, cytb, ND2, ATPase8/6, CO1, RAG-1, and IRBP genes; the GTR+G for the FIB7; and the HKY+G for the CO3. We did not phase nuclear gene sequences and we treated alignment gaps as missing data.

We performed maximum Likelihood analyses in RAxML v.7.0.3 [6] with 100 random addition replicates. We used a GTR+I+G model and we estimated parameters independently for each partition. We assessed the reliability of the ML tree by bootstrap analysis [7] including 1000 replications.

We inferred an ultrametric phylogeny using the Bayesian algorithms implemented in BEAST v.

1.6.1 [79]. Based on Ord and García-Porta [80] we set the mean global substitution rate to unity and produced an ultrametric tree with branch lengths expressed in units of substitutions per site; we modelled an uncorrelated branch rate variation using a lognormal distribution; and we used a Yule branching process with a uniform prior. Models and prior specifications applied were as follows (otherwise by default): GTR+I+G (12S, cytb, ND2, ATPase8/6, CO1, RAG-1, and IRBP), GTR+G (FIB7), HKY+G (CO3); Relaxed Uncorrelated Lognormal Clock (estimate); Yule process of speciation; random starting tree; alpha Uniform (0, 10); yule.birthRate (0, 1000). We run analyses four times for 5×10^7 generations with a sampling frequency every 10000 generations. Following [80], we used LogCombiner v. 1.6.1 to combine independent runs, which converged on very similar posterior estimates. We excluded the first 10% of generations as a burn-in phase for all runs; and we tested convergence and suitable mixing of the combined Markov Chain Monte Carlo chains using Tracer v. 1.5 [81]. We obtained a summary tree with mean node height computed using TreeAnnotator V. 1.6.1 (in the package BEAST), with a posterior probability limit set to 0.5. We considered nodes to be strongly supported if they received ML bootstrap values ≥ 70% and posterior probability (pp) support values ≥ 0.95 [82,83]. The alignment is available from TreeBASE (study ID 13646).

The alignment of the Columbiformes dataset included a total of 8950 base pairs (bp), 4362 bp of which corresponded to mitochondrial genes and 4588 bp to nuclear genes (see Table A3 for more details).

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Appendix S2: GenBank accession numbers of the sequences used for the inference of the phylogenetic relationships of Columbiformes.

Species	**ND2**	**cytb**	**12S**	**ATPCO3**	**COI**	**FIB7**	**RAG1**	**IRBP**
Alectroenas madagascariensis	—	AF483344	AF483307	—	—	—	—	—
Caloenas nicobarica	EF373326	AF483336	EF373289	EF373439	EF373363	EF373477	EF373493	EF373400
Chalcophaps indica	HM746789	AF483325	AF483288	—	EU541467	AY443694	—	—
Chalcophaps stephani	EF373328	AY443673	EF373293	EF373444	EF373365	AY443695	EF373498	EF373405
Claravis pretiosa	EF373329	AF182682	EF373294	EF373445	EF373366	AF182649	EF373499	EF373406
Columba arquatrix	EU481995	AF353412	—	—	—	EU482014	—	—
Columba bollii	EU481997	EU481983	—	—	—	EU482016	—	—
Columba guinea	EU482003	AF279708	—	—	—	EU482022	—	—
Columba junoniae	EU482004	EU481985	—	—	—	EU482024	—	—
Columba livia	AF353433	AF182694	EF373295	EF373446	EF373367	AF182661	EF373500	EF373407
Columba oenas	EU482007	EU481987	FN675576	—	GU571832	EU482025	—	—
Columba palumbus	EU482010	AF353411	AM902521	—	—	EU482032	—	—
Columba pulchricollis	AF353438	AF353413	—	—	—	—	—	—
Columba rupestris	AF353434	AF353410	—	—	—	GQ481610	—	—
Columba vitiensis	—	GU230687	GU230684	—	—	—	—	—
Columbina cruziana	—	AF483318	AF483294	—	—	—	—	—
Columbina inca	—	AF182683	—	—	—	AF182650	—	—
Columbina minuta	—	AF182685	—	—	—	AF182652	—	—
Columbina passerina	EU327611	AF182686	—	—	DQ433537	AF182653	—	—
Columbina picui	—	AF182687	—	—	FJ027423	AF182654	—	—
Columbina squammata	EF373330	AF182684	EF373296	EF373447	EF373368	AF182651	EF373501	EF373408
Columbina talpacoti	EU713836	EU442361	—	—	EU442319	—	—	—
Didunculus strigirostris	—	AF483343	AF483306	—	—	—	—	—
Drepanoptila holosericea	—	AF483345	AF483308	—	—	—	—	—
Ducula aenea	—	AF483331	AF483294	—	—	—	—	—
Ducula bicolor	—	AF182705	—	—	—	AF182672	—	—
Ducula melanochroa	GU230691	GU230690	GU230689	—	—	—	—	—
Ducula pacifica	—	AY443667	—	—	—	AY443689	—	—
Ducula pinon	—	AF483332	AF483295	—	—	—	—	—
Ducula pistrinaria	—	AY443669	—	—	—	AY443691	—	—
Ducula rubricera	GU230693	AY443668	GU230697	—	—	AY443690	—	—
Ducula rufigaster	EF373331	EF373277	EF373297	EF373448	EF373369	EF373479	EF373502	EF373409
Ducula zoeae	—	AF483333	AF483296	—	—	—	—	—
Ectopistes migratorius	—	AF483351	AF483314	—	—	—	—	—

Gallicolumba beccarii	HQ630220	AF483346	AF483309	—	—	AY443697	—	—
Gallicolumba canifrons	HQ630232	—	—	—	—	—	—	—
Gallicolumba criniger	HQ630225	—	—	—	—	—	—	—
Gallicolumba erythroptera	HQ630223	—	—	—	—	—	—	—
Gallicolumba hoedtii	HQ845209	—	—	—	—	—	—	—
Gallicolumba jobiensis	EF373332	EF373278	EF373298	EF373449	EF373370	EF373480	EF373503	EF373410
Gallicolumba keayi	HQ630236	—	—	—	—	—	—	—
Gallicolumba kubaryi	HQ630235	—	—	—	—	—	—	—
Gallicolumba luzonica	HQ630215	AF483334	AF483297	—	HM746790	—	—	—
Gallicolumba platenae	HQ630233	—	—	—	—	—	—	—
Gallicolumba rubescens	HQ630216	—	—	—	—	—	—	—
Gallicolumba rufigula	HQ630217	—	—	—	—	—	—	—
Gallicolumba sanctaecrucis	HQ630230	—	—	—	—	—	—	—
Gallicolumba stairi	HQ630230	—	—	—	—	—	—	—
Gallicolumba tristigmata	HQ630231	AF483319	AF483282	—	—	—	—	—
Gallicolumba xanthonura	HQ630222	—	—	—	—	—	—	—
Geopelia cuneata	HQ630221	AF483317	AF483280	—	—	AF182678	—	—
Geopelia striata	EF373333	EF373279	EF373299	EF373450	JF498863	EF373481	EF373504	EF373411
Geophaps lophotes	EF373334	AF483323	EF373300	EF373451	—	EF373482	EF373505	EF373412
Geophaps plumifera	HQ630226	AY443676	—	—	—	AY443698	—	—
Geotrygon albifacies	HQ993556	AY443658	—	—	—	AY443680	—	—
Geotrygon chiriquensis	HQ993548	AY443659	—	—	—	AY443681	—	—
Geotrygon costaricensis	HQ993549	AY443660	—	—	—	AY443682	—	—
Geotrygon frenata	HQ993550	HQ993508	—	—	—	HQ993564	—	—
Geotrygon goldmani	HQ993554	HQ993512	—	—	—	HQ993568	—	—
Geotrygon lawrencii	HQ993555	HQ993513	—	—	—	HQ993569	—	—
Geotrygon montana	EF373335	AF182696	EF373301	EF373452	—	AF182663	EF373506	EF373413
Geotrygon purpurata	HQ993552	HQ993510	—	—	—	HQ993566	—	—
Geotrygon saphirina	HQ993557	FJ899158	—	—	—	HQ993570	—	—
Geotrygon veraguensis	HQ993538	HQ993502	—	—	—	HQ993558	—	—
Geotrygon versicolor	—	AF483326	AF483289	—	—	—	—	—
Geotrygon violacea	HQ993551	HQ993509	NC015207	—	HQ993531	HQ993565	—	—
Goura cristata	EF373336	AF182709	EF373302	EF373453	EF373374	AF182676	EF373507	EF373414
Goura victoria	—	AF483320	AF483283	—	—	—	—	—
Gymnophaps albertsii	EF373337	EF373280	EF373303	EF373454	EF373375	EF373483	EF373508	EF373415
Hemiphaga chathamensis	HM165269	GQ912615	HM165267	—	HM165270	—	—	—
Hemiphaga novaeseelandiae	EF373338	AY443666	EF373304	EF373455	EU725864	AY443688	EF373509	EF373416
Henicophaps albifrons	EF373339	EF373281	EF373305	EF373456	EF373377	EF373484	EF373510	EF373417
Leptotila cassini	FJ175697	AY443661	—	—	—	AY443683	—	—
Leptotila jamaicensis	HQ993543	AF279706	—	—	—	—	—	—
Leptotila megalura	HQ993545	AF182697	AF483305	—	—	AF182664	—	—
Leptotila plumbeiceps	HQ993544	AF279707	—	—	—	—	—	—
Leptotila rufaxilla	EF373340	AF182698	EF373306	EF373457	FJ027742	AF182665	EF373511	EF373418

Leptotila verreauxi	FJ175693	AF279705	NC015190	—	DQ433767	HQ993559	—	—
Leucosarcia melanoleuca	EF373341	AF182712	EF373307	EF373458	EF373379	AF182679	EF373512	EF373419
Lopholaimus antarcticus	EF373342	EF373282	EF373308	EF373459	EF373380	EF373485	EF373513	EF373420
Macropygia amboinensis	EF373343	EF373283	EF373309	EF373460	EF373381	EF373486	EF373514	EF373421
Macropygia mackinlayi	AF353444	SF353415	—	—	—	—	—	—
Macropygia manadensis	EF373356	EF373287	EF373322	EF373473	EF373394	EF373491	EF373527	EF373434
Macropygia phasianella	—	AF182693	AF483302	—	—	AF182660	—	—
Macropygia tenuirostris	AF353445	AF353416	—	—	—	—	—	—
Metriopelia aymara	—	—	—	—	FJ027798	—	—	—
Metriopelia ceciliae	—	AF182688	—	—	—	AF182655	—	—
Metriopelia melanoptera	—	—	—	—	FJ027804	—	—	—
Metriopelia morenoi	EF373344	AY443677	EF373310	EF373461	EF373382	AY443699	EF373515	EF373422
Oena capensis	EF373345	AF182707	EF373311	EF373462	EF373383	AF182674	EF373516	EF373423
Otidiphaps nobilis	EF373346	AF483352	EF373312	EF373463	EF373384	EF373487	EF373517	EF373424
Patagioenas araucana	—	—	—	—	FJ027969	—	—	—
Patagioenas cayennensis	—	—	—	—	FJ027970	—	—	—
Patagioenas fasciata	AF353443	AF353414	—	—	DQ433886	AF353465	—	—
Patagioenas flavirostris	—	AY443656	—	—	DQ433887	AY443678	—	—
Patagioenas leucocephala	AY274070	AY274041	AY274023	—	—	AF182656	—	—
Patagioenas maculosa	—	—	—	—	FJ027973	—	—	—
Patagioenas oenops	AF353440	AF182690	—	—	—	AF182657	—	—
Patagioenas picazuro	—	—	—	—	FJ027974	—	—	—
Patagioenas plúmbea	AF251547	AF182691	—	—	—	AF182658	—	—
Patagioenas speciosa	EF373347	AF279711	EF373313	EF373464	—	AF279721	EF373518	EF373425
Patagioenas squamosa	—	AY443657	—	—	—	AY443679	—	—
Patagioenas subvinacea	AF353439	AF182692	—	—	—	AF182659	—	—
Petrophassa albipennis	EF373348	EF373284	EF373314	EF373465	EF373386	EF373488	EF373519	EF373426
Pezophaps solitaria	—	AF483337	AF483300	—	—	—	—	—
Phapitreron amesthystina	EF373349	AF182706	EF373315	EF373466	EF373387	AF182673	EF373520	EF373427
Phapitreron leucotis	—	AF279712	—	—	—	AY443692	—	—
Phaps chalcoptera	EF373350	AF182713	EF373316	EF373467	EF373388	AF182680	EF373521	EF373428
Ptilinopus leclancheri	—	AF182708	—	—	—	AF182675	—	—
Ptilinopus luteovirens	GU230703	GU230704	GU230707	—	—	—	—	—
Ptilinopus magnificus	GU230708	GU230709	GU230712	—	—	—	—	—
Ptilinopus melanospila	—	AF483328	AF483291	—	—	—	—	—
Ptilinopus occipitalis	—	AF493330	AF483293	—	—	—	—	—
Ptilinopus pulchellus	EF373351	EF373285	EF373317	EF373468	EF373389	EF373489	EF373522	EF373429
Ptilinopus rarotongensis	—	AY443663	—	—	—	AY443685	—	—
Ptilinopus Regina	GU230716	GU230715	GU230713	—	—	—	—	—
Ptilinopus richardsii	—	AY443664	—	—	—	AY443686	—	—
Ptilinopus rivoli	GU230717	GU230718	GU230721	—	—	—	—	—
Ptilinopus solomonensis	GU230726	—	GU230722	—	—	—	—	—
Ptilinopus superbus	—	AF483329	AF483292	—	—	—	—	—
Ptilinopus victor	GU230727	GU230728	GU230731	—	—	—	—	—
Raphus cucullatus	—	AF483338	AF483301	—	—	—	—	—

Reinwardtoena browni	EF373332	AF353417	EF373318	EF373469	EF373390	AF353468	EF373523	EF373430
Streptopelia bitorquata	AF353427	AF353406	—	—	—	—	—	—
Streptopelia capicola	EF373333	AF279709	EF373319	EF373470	—	AF279719	EF373524	EF373431
Streptopelia chinensis	AF353431	AF483341	AF483304	—	JF498900	AF182662	—	—
Streptopelia decaocto	AF353418	AF353398	—	—	GU571632	—	—	—
Streptopelia decipiens	AF353420	AF353400	—	—	—	—	—	—
Streptopelia hypopyrrha	AF353424	AF353403	—	—	—	—	—	—
Streptopelia mayeri	AF353429	AF483322	AF483285	—	—	—	—	—
Streptopelia orientalis	AF353426	AF353405	—	—	GQ482672	—	—	—
Streptopelia picturata	AF353430	AF353409	—	—	—	—	—	—
Streptopelia roseogrisea	AF353419	AF353399	—	—	—	—	—	—
Streptopelia semitorquata	AF353421	AF353401	—	—	—	—	—	—
Streptopelia senegalensis	AF353432	AF279710	—	—	HQ168039	—	—	—
Streptopelia tranquebarica	AF353428	AF353407	—	—	—	—	—	—
Streptopelia turtur	AF353425	AF353404	—	—	GU572103	—	—	—
Streptopelia vinacea	AF353423	AF353402	—	—	—	—	—	—
Treron australis	—	AF483349	AF483312	—	—	—	—	—
Treron calva	EF373354	AY443674	EF373320	EF373471	EF373392	AY443696	EF373525	EF373432
Treron sieboldii	AY274071	AY274042	AY274024	—	—	—	—	—
Treron vernans	—	AF483321	AF483284	—	—	AF182677	—	—
Treron waalia	—	AF483350	AF483313	—	—	—	—	—
Trugon terrestris	EF373355	EF373286	EF373321	EF373472	EF373393	EF373490	EF373526	EF373433
Turtur afer	—	AF483348	AF483311	—	—	—	—	—
Turtur brehmeri	—	AY151005	—	—	—	AY151006	—	—
Turtur chalcospilos	EF373357	AY443671	EF373323	EF373474	EF373395	AY443693	EF373528	EF373435
Turtur tympanistria	HM746793	HM746793	HM746793	HM746793	HM746793	—	—	—
Uropelia campestris	EF373358	EF373288	EF373324	EF373475	EF373396	EF373492	EF373529	EF373436
Zenaida asiática	AF251544	AF251533	—	—	DQ433271	AF258324	—	—
Zenaida auriculata	HM640211	AF182700	AF483303	—	HQ993524	AF182667	—	—
Zenaida aurita	AF251542	AF251532	—	—	—	AF182671	—	—
Zenaida galapagoensis	AF251540	AF251531	—	—	—	AF182668	—	—
Zenaida graysoni	AF251537	AF182702	—	—	—	AF182669	—	—
Zenaida macroura	EF373359	AF182703	EF373325	EF373476	EF373397	AF258321	EF373530	EF373437
Zenaida meloda	AF251545	AF182699	—	—	—	AF182666	—	—
Outgroups:								
Anhima cornuta	AY140737	AY140735	AY140699	EF373438	AY140729	AY140701	AY140765	EF373399
Caprimulgus vociferus	EF373327	U89194	EF373292	EF373443	EF373364	AY695136	EF373497	EF373404
Chaetura pelagica	AY294537	AY294475	EF373291	EF373441	EF373361	AY830606	EF373495	EF373402
Crax blumenbachii	AY140747	AF165468	AF165444	AY143682	AF165492	AY140711	AY140775	EF373398
Gallus gallus	NC001323	NC001323	NC001323	NC001323	NC001323	AY082425	AF143730	AY994153
Hirundapus caudacutus	AY294536	AY294474	EF373290	EF373440	EF373360	EF373478	EF373494	EF373401
Podargus strigoides	—	EF373276	—	EF373442	EF373362	AY082408	EF373496	EF373403
Struthio camelus	NC002785	NC002785	NC002785	NC002785	NC002785	AY082424	AF143727	—

Appendix S3: Information on the length, variability and models applied to each one of the 9 independent partitions used in the phylogenetic analyses.

	Number of sequences	% of missing data	Number of aligned sites	Parsimony-informative sites	Variable sites	Best model
12S	87	47	620	224	296	GTR+I+G
Cytb	144	12.2	1042	485	547	GTR+I+G
ND2	121	26.3	1040	609	684	GTR+I+G
ATP-8/6	43	73.8	842	413	485	GTR+I+G
CO3	42	73.8	173	77	91	HKY+G
CO1	62	62.2	645	237	275	GTR+I+G
FIB7	93	46	1051	547	801	GTR+G
RAG-1	42	74	2733	455	982	GTR+I+G
IRBP	41	75	804	126	255	GTR+I+G
All 9 partitions			8950	3173	4416	

Appendix S4: Species morphological and foraging strategy traits. Morphological traits are shown in millimetres and body mass data are shown in grams.

Species	**tarsus**	**tail**	**wing**	**beak**	**mass**	**foraging strategy**
Alectroenas madagascariensis	36	100	175	16	173	mainly arboreal
Caloenas nicobarica	37	78	253.5	23	530	mainly terrestrial
Chalcophaps indica	21	84.5	151	15	131.5	mainly terrestrial
Chalcophaps stephani	21.5	78	139	17	122	mainly terrestrial
Claravis pretiosa	20	64.5	170	12.5	64.5	mainly terrestrial
Columba arquatrix	26	135	221	24	358.5	generalist
Columba bollii	26	156.5	214.5	19.5	NA	generalist
Columba guinea	25	110.5	228	21	300	mainly terrestrial
Columba junoniae	24	151.5	220.5	19	NA	mainly arboreal
Columba livia	30.5	102.5	222.5	18	270	mainly terrestrial
Columba oenas	27	108	219.5	19.5	303.5	mainly terrestrial
Columba palumbus	26.5	139.5	247	20.5	519.5	generalist
Columba pulchricollis	24	115	210.5	17.5	330	generalist
Columba rupestris	26.5	112.5	222.5	17.5	245.5	mainly terrestrial
Columba subvinacea	24	130	165	15	170	mainly arboreal
Columba vitiensis	27.5	133	232.5	20	389.5	generalist
Columbina cruziana	11	29.5	83	13	47	mainly terrestrial
Columbina inca	7.5	57.5	96.5	10	48	mainly terrestrial
Columbina minuta	6.5	29.5	64.5	7	34	mainly terrestrial
Columbina passerina	7.5	30	78	10	32	mainly terrestrial
Columbina picui	9.5	51	92	10	52	mainly terrestrial
Columbina squammata	7.5	66	94	10.5	54	mainly terrestrial
Columbina talpacoti	10	50	75.5	10.5	49	mainly terrestrial
Didunculus strigirostris	38.5	98.5	197	19	400	generalist
Drepanoptila holosericea	28	72.5	149.5	15	190	mainly arboreal
Ducula aenea	28.5	133	237.5	24	549.5	mainly arboreal
Ducula bicolor	28	118	232	20.5	487.5	mainly arboreal
Ducula melanochroa	35.5	143.5	240.5	22.5	661	mainly arboreal
Ducula pacifica	32	126	236.5	23	395	mainly arboreal
Ducula pinon	34.5	131.5	259.5	23.5	802	mainly arboreal
Ducula pistrinaria	31	142.5	243	23	485	mainly arboreal
Ducula rubricera	31.5	122	245.5	28	675	mainly arboreal
Ducula rufigaster	27	108.5	202	17	498	mainly arboreal
Ducula zoeae	28.5	120	223.5	21.5	592	mainly arboreal
Ectopistes migratorius	26.5	192.5	199	16.5	298.5	generalist
Gallicolumba beccarii	26.5	60.5	105	15.5	81.5	mainly terrestrial
Gallicolumba canifrons	30	63	118	18	NA	mainly terrestrial
Gallicolumba criniger	33	97	165	18	192.5	mainly terrestrial
Gallicolumba erythroptera	30	70.5	145	19.5	113.5	mainly terrestrial
Gallicolumba hoedtii	26.5	95.5	149	19.5	NA	mainly terrestrial

Gallicolumba jobiensis	23.5	70.5	147	18.5	142	mainly terrestrial
Gallicolumba keayi	32	65	142	16	NA	mainly terrestrial
Gallicolumba kubaryi	31	77	149	21	NA	mainly terrestrial
Gallicolumba luzonica	31.5	92	144	19	133	mainly terrestrial
Gallicolumba platenae	33	100	147.5	20	NA	mainly terrestrial
Gallicolumba rubescens	25.5	71.5	124.5	17	60	mainly terrestrial
Gallicolumba rufigula	29	69	132.5	19	129	mainly terrestrial
Gallicolumba sanctaecrucis	22.5	68.5	136.5	18	NA	mainly terrestrial
Gallicolumba stairi	31	91	147	21.5	171	mainly terrestrial
Gallicolumba tristigmata	41	112	177	23	275	mainly terrestrial
Gallicolumba xanthonura	28	86.5	140	20	106	mainly arboreal
Geopelia cuneata	14	102.5	91	10.5	30	mainly terrestrial
Geopelia striata	19	95	101	14	56	mainly terrestrial
Geophaps lophotes	20.5	134	164.5	15	175	mainly terrestrial
Geophaps plumifera	21	65	108	14	83	mainly terrestrial
Geotrygon albifacies	42.5	75	160	17	155	mainly terrestrial
Geotrygon chiriquensis	41.5	54	155.5	18	301.5	mainly terrestrial
Geotrygon costaricensis	40.5	73.5	139	14	277.5	mainly terrestrial
Geotrygon frenata	41.5	54	155.5	18	301.5	mainly terrestrial
Geotrygon goldmani	39.5	65	149.5	16	258	mainly terrestrial
Geotrygon lawrencii	38	74.5	142.5	15	220	mainly terrestrial
Geotrygon montana	25	54.5	140	13.5	127.5	mainly terrestrial
Geotrygon purpurata	29.5	20	133.5	18	NA	mainly terrestrial
Geotrygon saphirina	31	21	139	19	203	mainly terrestrial
Geotrygon veraguensis	36	35	190	17	155	mainly terrestrial
Geotrygon versicolor	34	54	167	14	225	mainly terrestrial
Geotrygon violacea	32.5	67	150	16	121.5	mainly terrestrial
Goura cristata	92	255	362.5	31.5	2100	mainly terrestrial
Goura victoria	91.5	287	375	33.5	2384	mainly terrestrial
Gymnophaps albertisii	23	123.5	206.5	15.5	259	mainly arboreal
Hemiphaga chatmanensis	37.4	201	267	19.8	NA	mainly arboreal
Hemiphaga novaeseelandiae	34.3	181	258	16	725	mainly arboreal
Henicophaps albifrons	29	125	199	31.5	247	mainly terrestrial
Leptotila cassini	30	45.5	133	13	155.5	mainly terrestrial
Leptotila jamaicensis	30	65	158.5	16	190	mainly terrestrial
Leptotila megalura	29.5	70	151.5	15	145	mainly terrestrial
Leptotila plumbeiceps	29.5	50	140.5	12	172	mainly terrestrial
Leptotila rufaxilla	28	74.5	141	15.5	149	mainly terrestrial
Leptotila verreauxi	30	66.5	143.5	14.5	126.5	mainly terrestrial
Leucosarcia melanoleuca	36.5	127	194	23	415	mainly terrestrial
Lopholaimus antarcticus	32.5	170.5	266.5	27	537.5	mainly arboreal
Macropygia amboinensis	17.5	181	176	15	143	mainly arboreal
Macropygia mackinlayi	14.5	157.5	156	11.25	87	mainly arboreal
Macropygia phasianella	19.5	196	187	16	200	mainly arboreal
Macropygia tenuirostris	16.5	174	178	14.5	174	mainly arboreal

Metriopelia aymara	11	39.5	110.5	11	61.8	mainly terrestrial
Metriopelia ceciliae	14	53.5	92	10	59	mainly terrestrial
Metriopelia melanoptera	14	71	121	11.5	119	mainly terrestrial
Metriopelia morenoi	11.5	65.5	99.5	12	NA	mainly terrestrial
Oena capensis	15	140.5	107	14	41	mainly terrestrial
Otidiphaps nobilis	56.5	172	196.5	26.5	500	mainly terrestrial
Patagioenas araucana	27	135	215	16	NA	generalist
Patagioenas cayennensis	36	125	185	17	214.5	generalist
Patagioenas fasciata	21.5	132	214	18	343	mainly arboreal
Patagioenas flavirostris	25	135	198	15	346	generalist
Patagioenas leuconota	29	112	234.5	18	281	mainly terrestrial
Patagioenas maculosa	22	140	225.5	19.5	326.5	mainly terrestrial
Patagioenas oenops	30	135	200	17	265	generalist
Patagioenas picazuro	27.5	110	229.5	19	402	generalist
Patagioenas plumbea	27	150	180	18	170	mainly arboreal
Patagioenas speciosa	18	117	185	18	287.5	mainly arboreal
Patagioenas squamosa	22	140	212.5	16.5	288	generalist
Petrophassa albipennis	21	106	136	15	141.5	mainly terrestrial
Phapitreron amethystina	20	87	147	23	142.5	mainly arboreal
Phapitreron leucotis	17.5	84	129.5	16.5	145	mainly arboreal
Phaps chalcoptera	25.5	114	203.5	21	260	mainly terrestrial
Ptilinopus leclancheri	21	88.5	141	16	163.5	mainly arboreal
Ptilinopus luteovirens	21	55.5	121	13.75	NA	mainly arboreal
Ptilinopus magnificus	31	172.5	223	22.5	360	mainly arboreal
Ptilinopus melanospila	16.5	68.5	114	12	92	mainly arboreal
Ptilinopus occipitalis	22.5	100.5	159.5	16	247.5	mainly arboreal
Ptilinopus pulchellus	17.5	58.5	105.5	13	72	mainly arboreal
Ptilinopus rarotongensis	23.5	87	133	10	NA	mainly arboreal
Ptilinopus Regina	19	71.5	129	13	115	mainly arboreal
Ptilinopus richardsii	19.5	63.5	127	11.5	99	mainly arboreal
Ptilinopus rivoli	20	73.5	139.5	16	145	mainly arboreal
Ptilinopus solomonensis	17	64	119.5	13.5	97.5	mainly arboreal
Ptilinopus superbus	19	64	127.5	15	118	mainly arboreal
Ptilinopus victor	20	55.5	119	13.5	NA	mainly arboreal
Reinwardtoena browni	19	193	278.5	19	302	mainly arboreal
Streptopelia bitorquata	20.5	120.5	163.5	17.5	160	mainly terrestrial
Streptopelia capicola	24	111.5	151.5	15.5	114	mainly terrestrial
Streptopelia chinensis	22	134.5	322.5	16	172	mainly terrestrial
Streptopelia decaocto	20	121.5	172.5	15.5	186	mainly terrestrial
Streptopelia decipiens	25.5	133.5	177.5	17.5	185	mainly terrestrial
Streptopelia hypopyrrha	25	124	179	17.5	162	mainly terrestrial
Streptopelia mayeri	34.5	162.5	203.5	23	311.5	generalist
Streptopelia orientalis	21.5	114	187.5	16.5	219.5	mainly terrestrial
Streptopelia picturata	30	130	165	18	182	mainly terrestrial
Streptopelia roseogrisea	27	110	163.5	16	155	mainly terrestrial

Streptopelia semitorquata	25	126	191	22	244	mainly terrestrial
Streptopelia senegalensis	22.5	111	136.5	18.5	95	mainly terrestrial
Streptopelia tranquebarica	14.5	81.5	134	13	104	mainly terrestrial
Streptopelia turtur	18.5	98	296.5	16	135.5	mainly terrestrial
Streptopelia vinacea	20.5	93.5	138.5	12	110.5	mainly terrestrial
Treron australis	40	120	175	18	210	mainly arboreal
Treron calva	21.5	85	157	24.5	207.5	mainly arboreal
Treron sieboldii	21.5	112.5	187.5	19	245	mainly arboreal
Treron vernans	20	80	148.5	15.5	132.5	mainly arboreal
Treron waalia	26.5	102.5	177	16	259.5	mainly arboreal
Trugon terrestres	42.5	111	172.5	23.5	361.5	mainly terrestrial
Turacoena manadensis	17	190	205	18	212.5	mainly arboreal
Turtur afer	17.5	85	110.5	15	63.5	mainly terrestrial
Turtur brehmeri	24.5	103	131.5	19.9	112.5	mainly terrestrial
Turtur chalcospilos	18	82	112	18	60	mainly terrestrial
Turtur tympanistria	21.75	78.5	115.5	15.25	71.5	mainly terrestrial
Uropelia campestris	8.5	55.5	64	9.5	28	mainly terrestrial
Zenaida asiática	32	79	161	18	156	mainly terrestrial
Zenaida auriculata	27	86.5	149	16	150	mainly terrestrial
Zenaida aurita	23	84.5	158	15	150	mainly terrestrial
Zenaida galapagoensis	27	38.5	144.5	16.5	79.5	mainly terrestrial
Zenaida graysoni	31	93	154	17	190	mainly terrestrial
Zenaida macroura	20.5	89.5	139	13.5	135	mainly terrestrial
Zenaida meloda	28	83	166.5	18	209.5	mainly terrestrial

Appendix S5: Disparity analyses. Measures of total morphological disparity within every log-transformed morphological trait included. Results are presented for all Columbiformes for which morphological information was available, and only including species sampled in the phylogeny using "disp.calc" function in GEIGER package (Harmon et al. 2008).

		Disparity	
Trait	Groups	All species	Species within phylogeny
TARSUS	All	0.711119	0.647763
	Terrestrial	1.293159	0.455233
	Generalist	0.299645	0.05026
	Arboreal	0.321562	0.138509
	Generalist+Arboreal	0.32529	0.127587
TAIL	All	1.027703	0.886566
	Terrestrial	0.989073	0.455296
	Generalist	0.298438	0.055023
	Arboreal	0.817009	0.283525
	Generalist+Arboreal	0.767217	0.243757
WING	All	0.540931	0.400823
	Terrestrial	0.636274	0.212051
	Generalist	0.110129	0.011963
	Arboreal	0.412382	0.145979
	Generalist+Arboreal	0.377117	0.125881
BEAK	All	0.354225	0.2517
	Terrestrial	0.464051	0.141639
	Generalist	0.145476	0.037608
	Arboreal	0.303569	0.112586
	Generalist+Arboreal	0.276619	0.096129

Appendix S6: Mean, standard deviation, median, modal number, maximum and minimum number of evolutionary transitions between the different foraging strategy categories from the stochastic character mapping reconstruction of changes in foraging behaviour computed from all 500 sampled maps derived from the ultrametric Bayesian analysis in BEAST.

	terrestrial to generalist	terrestrial to arboreal	generalist to terrestrial	generalist to arboreal	arboreal to terrestrial	arboreal to generalist
mean	5.18	4.55	3.04	5.05	0.07	0.17
median	5	5	3	5	0	0
SD	1.85	1.27	1.17	1.52	0.36	0.62
modal number	7	5	2	6	0	0
max	9	9	6	10	5	4
min	2	1	0	0	0	0

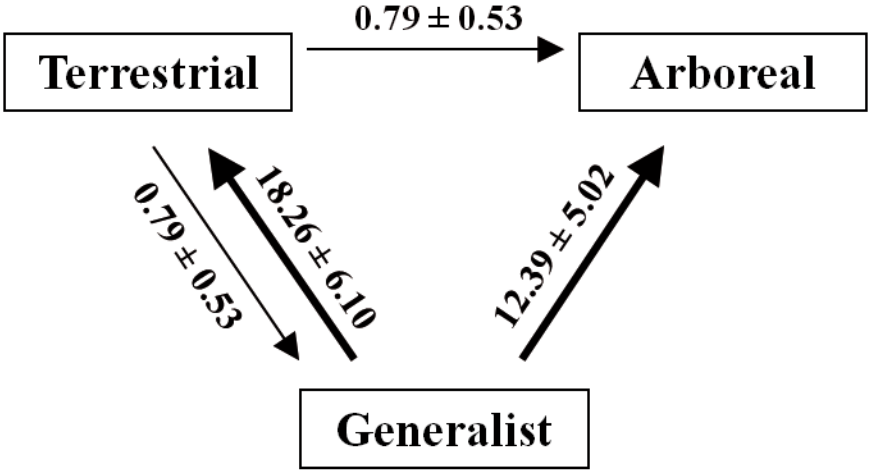
Appendix S7: Test of evolutionary transition rates of behavioural changes

To formally test if lineages under certain selective regimes tended to change foraging behaviour more frequently than others, or if some evolutionary paths were restricted we estimated the evolutionary transition rates between all foraging strategy categories with a phylogenetic Bayesian Markov Chain Monte Carlo (MCMC) method to derive point estimates of log-likelihoods and the parameters of statistical models, as implemented in the multi-state option from BayesTraits [84]. To specifically validate the hypothesis that some transitions are significantly more probable than others, we computed likelihood ratio tests comparing different evolutionary scenarios [84]. First, we investigated if there were differences in evolutionary transition rates among foraging strategies by comparing a complete model including all six transition rates with a null model where all transitions were restricted to be the same. Then, to specifically address whether transitions from generalist to specialist foraging strategies were more probable than transitions from specialist to generalist, we computed likelihood ratio tests comparing the complete model to models where transitions in both directions were assumed to be equal [84]. Finally, we asked if some particular evolutionary transitions were very unlikely to occur by forcing them to be 0 and then comparing their fit with the complete model. If these models do not differ significantly this is taken as evidence that the transition rate does not differ from zero.

The results (Figure below) show that probabilities for generalist foragers to evolve to a specialist foraging strategy were much higher than the chances for both terrestrial specialist ($p < 0.001$; Figure below) and arboreal specialist ($p < 0.005$) to become generalist. In contrast, evolutionary transitions from an arboreal foraging behaviour to either terrestrial or generalist behaviour were non-significantly different from zero ($p > 0.05$ in both cases) further supporting that arboreal foraging may be an evolutionary dead-end (Figure below).

□, e□Ur Age□D, òC D□e- ò0AcJòM□ E□g□ eD□ot□cg□M DJcJòM□□ecC eeM□tòg□ JMr□Dcg□ er E□1□ eròg]eD□ eDcJ3 □ eB□ADJMr□□ □□ □□□□ eDJ□M □ge1òMDcgA1cJòM□JM□□□EeD□g□ cD□tgò3 □□ g□M Bò3 □D□ : 0e□ òt□WN□ , E0òr eMecJ1□cgeeDk□□g□M DJcJòMD□M□cg□e: geDeMceB□□E□□M □□ gòC □Bò□M□c□DJr MtJ1□M cOE□ BJtteg□tgò3 □N□□M B□□ò0B□□ggòC D□1òggeD. òMB□cò□cg□MDJcJòMD□c, □ □□ e□DJr MtJ1□M cOE□3 òge□ : gò□□ 0e□cò□ò11Ag□c, □M □c, e□òMeD□òM□c, e□ò: : òDJce□BJge1cJòM□

□



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YH□ □□r eOS□ k□ □□ e□Be5□□k□ NN; □□□EeD□M□□M□0EDJD□ot□1ògge0□ceB□e- ò0AcJòM□ot□BJD1gece□1, □g□1cegD□□E□ ge- egD□□0e6dA3 : □□ □g2ò- □1, □JM□□ òMce□□□gOk□*g □rS□□ □□ □dor□nSad*□) ú5□YNY7Yz Wk□□

□ □

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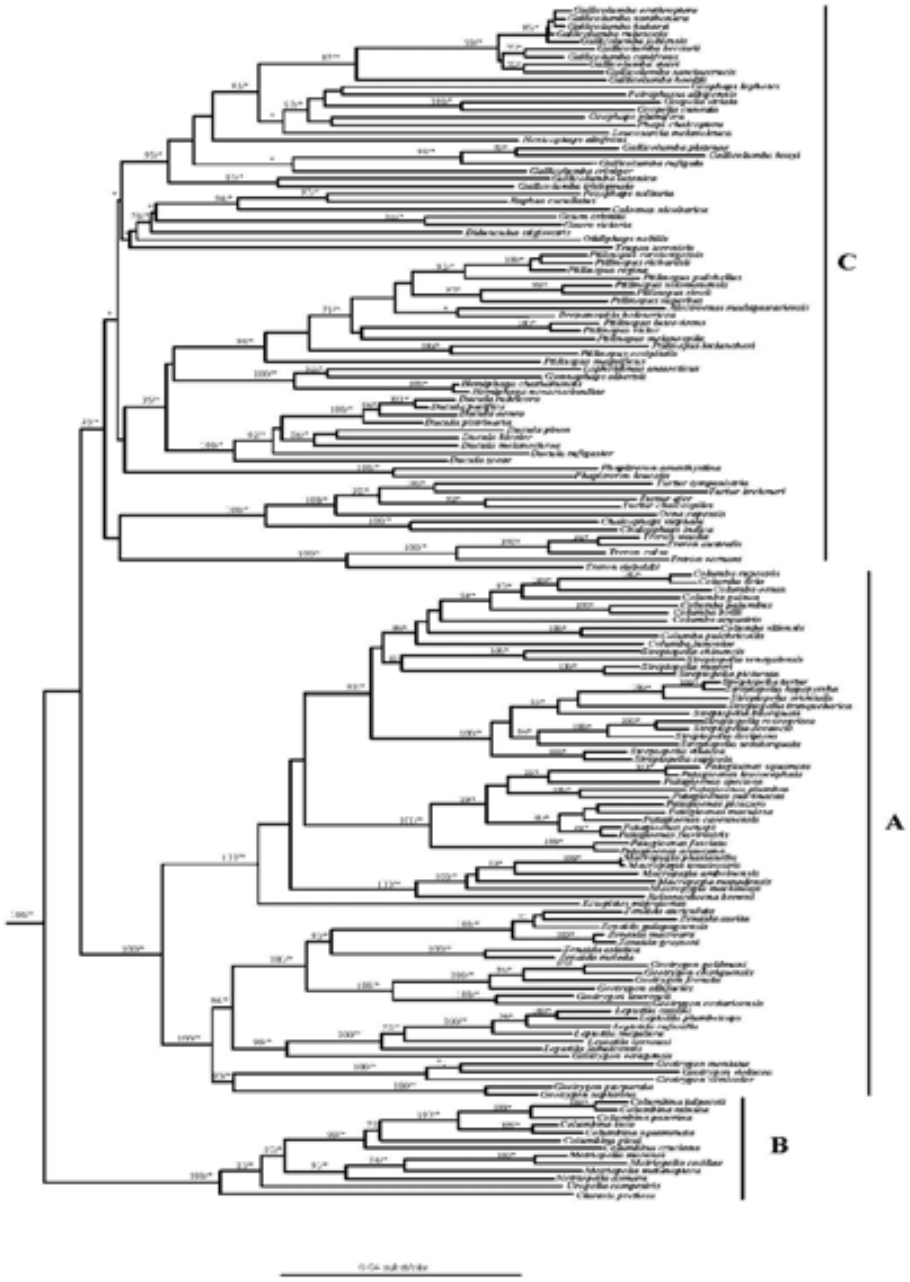
Appendix S8: Percentage explained by each PCA axis and eigenvector scores from the phylogeny-corrected PCA after phylogenetic size-correction.

		PC1	PC2	PC3
% explained		48.2	31.1	11.5
eigenvectors	tarsus	-0.397	0.819	0.333
	tail	-0.864	-0.482	0.146
	wing	-0.158	0.063	-0.785
	beak	-0.267	0.304	-0.502

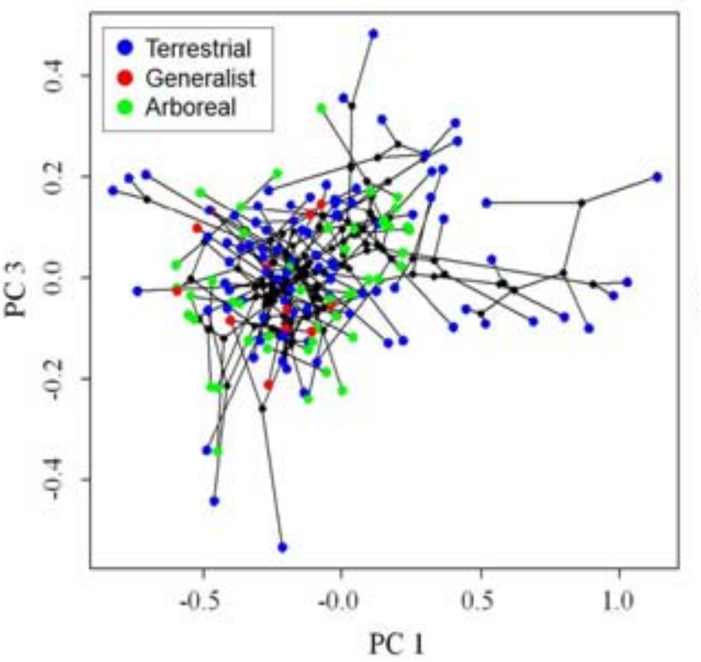
Appendix S9: Hansen phylogenetic half-life describing the time required to traverse half the morphological distance from the ancestral state to the optimum. Here this is expressed with no time units and results are expressed for relative comparison purposes only

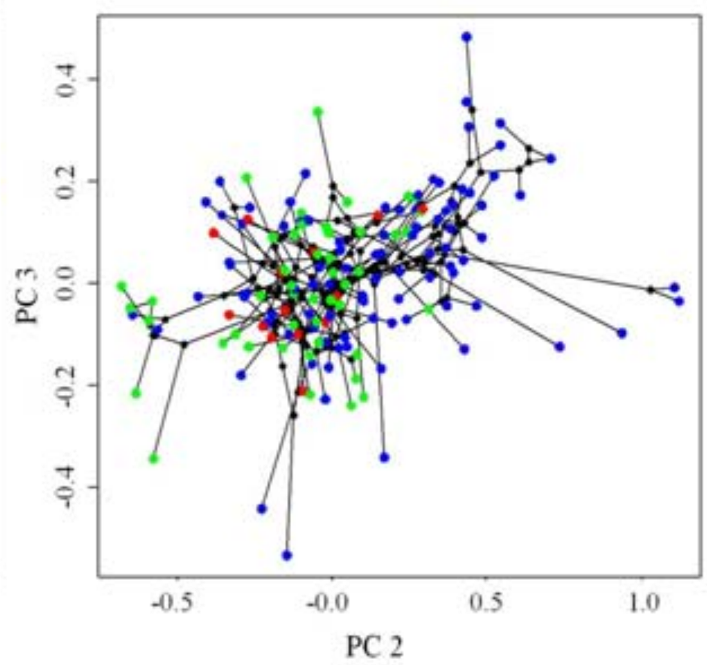
	phylogenetic half life ($t_1/_2$)		
	terrestrial	generalist	arboreal
PC1	0.065	0.029	0.028
PC2	0.097	0.051	0.047
PC3	0.027	0.032	0.03
body size	0.175	0.042	0.045

Figure B: Maximum likelihood (ML) phylogenetic tree of 154 Columbiformes based on 8950 bp of concatenated sequences of six mitochondrial (12S, cytb, ND2, ATPase8/6, CO3, and CO1) and three nuclear (FIB7, RAG-1 and IRBP) genes. Eight specimens of the genera *Anhima, Caprimulgus, Chaetura, Crax, Gallus, Hirundapus, Podargus* and *Struthio* were used to root the tree and have not been included in the figure (see Table S2). Tree topology and branch lengths are for the sampled tree with the highest likelihood by RaxML (100 searches, log likelihood = -126492.974854). Maximum-likelihood bootstrap support value above 70% and posterior probability values ≥ 0.95 of the Bayesian analysis using BEAST are indicated above branches. Clades A, B and C, correspond to Pereira et al. 2007.

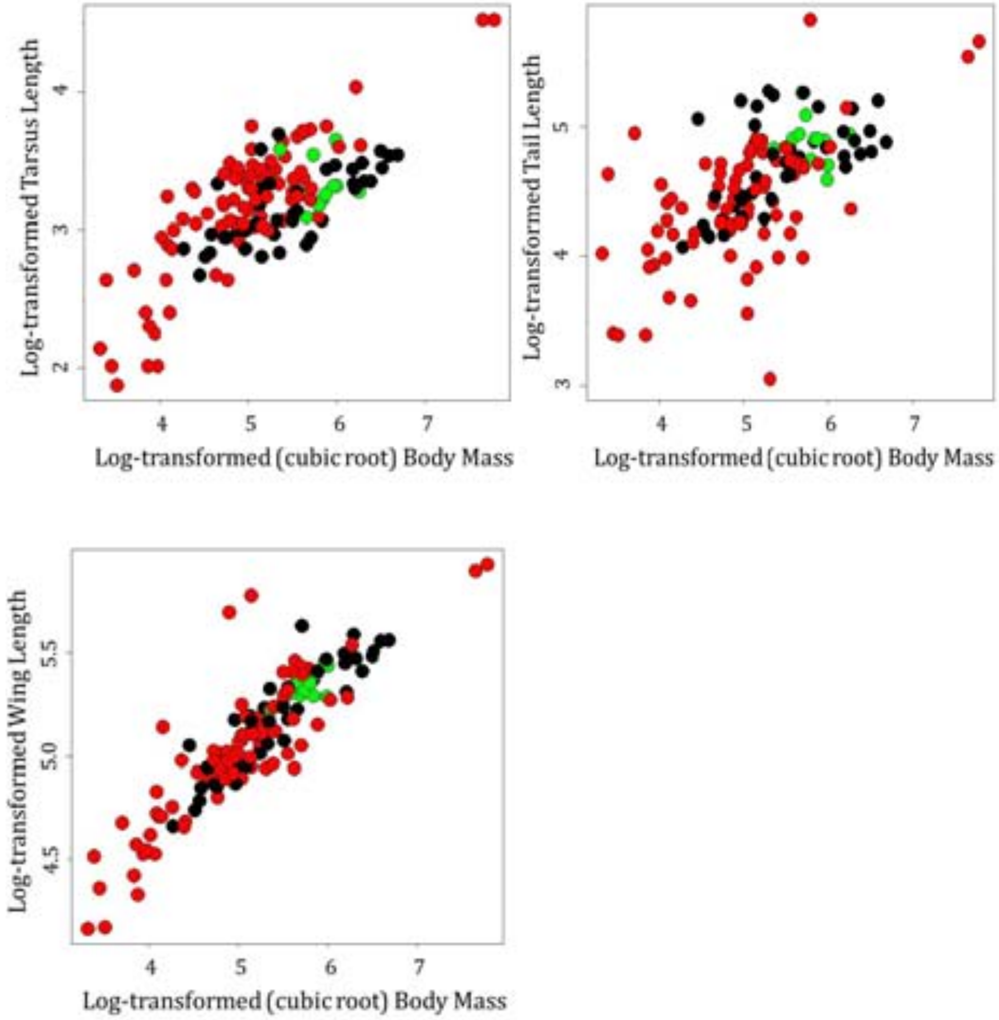


Figures C1 and C2: A phylogenetic morphospace representation of all 154 Columbiformes that superimposes the branching patterns of the phylogeny (black lines) on the plot of the two first PC axes from the phylogenetic PCA. Species are colored with respect to their foraging behavior category: terrestrial (blue), (green) and generalist (red). Figure C1 shows represents PC1 vs. PC3 Figure C2 illustrates PC2 vs. PC3





Figures C3 a, b, and c: Scatterplot of 154 Columbiformes species' scores on morphological distribution for log-transformed tarsus (C3a), tail (C3b), and wing (C3c) lengths against log-transformed cubic root of the bodymass. Colors indicate foraging strategy states: terrestrial lineages (red), arboreal (black) and generalist (green).



Chapter 3

Integrating the role of geography, ecology and behavior in the adaptive diversification of a major avian clade [2]

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[1] With Daniel Sol and Trevor Price. To be submitted

Abstract

Although behavior has long been viewed as an important driver of evolutionary change, most evolutionary theory has been developed under the view that organisms are passive agents of selection. However, by changing their behavior animals are able to shape the selective pressures that affect them, and hence intrinsic forces can also be important in driving evolution. Our aim here is to provide an integrative perspective of whether and how behavioral shifts interact with extrinsic factors in driving evolutionary change. We extend previous work in a major bird clade by asking in what geographic and ecological context behavioral changes take place and find that they do not occur –and become fixed within populations- at random. Rather, they are largely associated with range expansions. Specifically, evolutionary transitions on the foraging behavior of Columbiformes only occurred in islands, where animals encounter novel ecological opportunities that drive changes in the direction of selective pressures. Evolutionary models confirm that the colonization of islands accelerated the rate of morphological evolution for a functionally-relevant trait, again consistent with the behavioral drive hypothesis. Finally, we found that the acquisition of an arboreal foraging also spurred speciation rates, which has led to the large number of extant arboreal species through increased dispersal ability. Thus, both intrinsic and extrinsic forces seem critical to explain the evolutionary diversification of animals and should be integrated in studies investigating with the causes of animal evolutionary diversification.

Introduction

Researchers have long been fascinated by the extraordinary variety of life forms, but understanding why and how lineages diversify in phenotype and species numbers remains a major challenge in evolutionary biology. This is because the process of evolutionary diversification is complex, involving a variety of geographic and ecological factors as well as organism's features that can either facilitate or constraint evolutionary change. As a consequence of such complexity, there is probably not a single answer to explain why and how organisms diversify (Gavrilets & Losos 2009).

However, some evolutionary generalities apply to many groups of animals. For example, the existence of ecological opportunities has been long assumed to facilitate evolutionary change because they drive a change in the selective forces acting on populations, pulling populations' phenotypes towards new evolutionary directions. Ecological opportunities conductive to adaptive diversification can arise as a result of the colonization of remote areas with impoverished biota (e.g. inter-specific competition or decreased predation (Van Valen 1965)). They can also be the consequence of evolutionary innovations, the emergence of new – previously inexistent- ecological opportunities, and the massive extinction of competitor species (Losos & Mahler 2010).

The relative role of each of these factors may vary in different groups and scenarios. In birds, range expansions have been shown to be a major factor in diversification. For example, Phillimore et al. (2006a) identified dispersal ability as the most important ecological trait associated to species' diversification in birds. The probabilities of a lineage to diversify are thus greatly predicted to depend on its ability to arrive to new areas. However, in most of such scenarios, the simple existence of new ecological opportunities is not enough to change the selective pressures acting in a population. Rather, a behavioral shift is needed to take profit from such new opportunities, allowing for subsequent modifications on selective pressures (Mayr 1963). Surprisingly, the importance of behavioral changes in evolution has been largely ignored in evolutionary studies (Lapiedra et al. 2013). As suggested by Price referring to species' diversification "reaching a new area (…) is only half the battle" (Price 2008). Once a population arrives into a new area, the ability of individuals to adjust their behavior in adaptive ways will determine whether and how they are able to deal with changes in the distribution of resources, competition regimes, predation pressures, and the existence of new parasites (Baldwin 1896; MacArthur & Wilson 1967).

One of the issues that have hindered the incorporation of behavior into evolutionary studies is that empirical evidence is scarce. The only support to date was evidence that in birds, large brained lineages have experienced a greater taxonomic and morphological diversification than small brained lineages (Sol et al. 2005d; Sol & Price 2008). Assuming that brain size reflects behavioral flexibility, this can be taken as indirect evidence for the behavioral drive hypothesis. The problem is that behavior can affect evolution by other mechanisms than by exposing individuals to new selection pressures, for example by facilitating the colonization of new regions (Sol et al. 2005a; Price 2008). Moreover, the alternative that behavior inhibits instead of promotes evolutionary change is also possible because behavior itself is an important way through which animals respond to new ecological pressures, for example allowing individuals to find novel foods when the traditional ones are scarce. Thus, behavioral shift may also reduce the strength of natural selection by hiding genetic variation from natural selection, and hence inhibiting evolutionary change - the so-called Bogert effect- (Bogert 1949; Robinson & Dukas 1999; Price et al. 2003).

In a recent study in pigeons and doves, Lapiedra et al. (2013) used a more direct approach to test the behavioral drive hypothesis. Using evolutionary reconstructions and adaptive models, they found that behavioral changes have led to associated evolutionary responses in functionally relevant morphological traits, accelerating the rates of phenotypic evolution (Lapiedra et al. 2013), consistent with the behavioral drive hypothesis (Wyles et al. 1983; Sol et al. 2005b). Specifically, changes from terrestrial to arboreal foraging behavior reconstructed in a set of phylogenies brought associated shorter tarsi and longer tails, consistent with functional predictions. Interestingly, increased morphological specialization in arboreal lineages seems to have subsequently constrained reversals to terrestrial foraging (Lapiedra et al. 2013).

Our aim is to provide a more holistic perspective that allows us to fully integrate for the first time the role of behavioral changes in evolutionary diversification. To do this, we need to specifically show not only how such behavioral changes help animals dealing with new ecological pressures, but also how such behavioral modifications interact with other key biogeographic and ecological factors to govern the process of adaptive diversification. Thus, here we extend previous work in pigeons and doves by asking in what geographic and ecological context behavioral changes play a major role in evolution. Our prediction is that behavioral changes may not occur –and become fixed in a population- at random. Rather, they may depend under certain ecological conditions. We investigate if inhabiting islands, having different diets, living in different latitudes or habitat types influences the occurrence of behavioral changes from terrestrial to arboreal habits. Islands have been classically viewed as a factor promoting evolutionary divergence because they offer ecological opportunities and facilitate genetic isolation (MacArthur & Wilson 1967; Losos & Ricklefs 2009). Different habitats can also to some extent promote evolutionary divergence (e.g. Price et al. (2011)) and reproductive isolation (Mayr 1963), but can also affect diversification by limiting the opportunities available for species. We focus on their consequences for adaptive diversification and speciation. Finally, we hypothesize that changes in biogeographic, ecological and behavioral factors may have affected evolution of pigeons and doves in terms of species numbers and we test for differences in speciation rates among groups within the lineage.

A major difficulty for a study like ours is inferring past evolutionary events using information on contemporary species. We tackle this limitation by using a stochastic character mapping approach that takes into account phylogenetic uncertainty by considering a number of different phylogenetic hypotheses from Bayesian estimations. Using a complete phylogeny of Columbiformes, we use this approach to reconstruct the evolutionary transitions between island-mainland, habitats and foraging behavior. We then use such reconstructions to investigate the relative influence of these traits in the evolutionary diversification of pigeons and doves. This major bird clade is suitable to validate the questions stated above because behavioral changes have been shown to affect evolutionary change of this clade (Lapiedra et al. 2013) and they have a remarkable dispersal ability (Pereira et al. 2007) that has allowed them to successfully colonize many islands: in fact, more than half of the > 300 species inhabit exclusively islands (Gibbs, D., Barnes, E., Cox, J. 2001).

Material and methods

Ecological and morphometric information

The foraging niche of species was defined as the frequency of use of the two foraging strategies (i.e. terrestrial or arboreal) and the two types of resources (i.e. fruit vs. grain and seeds). We quantified the frequency of use in an ordinal scale depending on whether either the strategy or resource was not used at all (0.0), occasionally used (0.1), frequently used (0.5), and almost exclusively used (1.0). In addition, we collected information on the condition and degree of insularity, qualified as whether the species occurs exclusively on islands and main habitat category. Information was mainly obtained from Gibbs et al. (2001). Some variables were reclassified for some analyses where variables were to be ordered as belonging to only two categories. For such analyses, we classified members of the clade as terrestrial V*s* arboreal, frugivorous V*s* granivorous, island V*s* mainland inhabitants, and species inhabiting open Vs forested habitats.

The continuous morphological variables assembled for the analysis included the length of the wing, tail, tarsus and beak (in mm). Morphological values were log-transformed for statistical purposes. Morphometric information was also primarily obtained from Gibbs et al. (2001) and Dunning (2008). Then we conducted a phylogenetic size-correction from the logarithms of raw data and we built a phylogenetic PCA using the "phylo.pca" function in Phytools (Revell 2009) including the measurements of the four morphological traits analyzed to describe the morphological variation in a multivariate fashion. This takes into account the phylogenetic relatedness between species by incorporating a variance-covariance matrix for computing the scores of each axis (Revell 2009).

Phylogenetic hypothesis

We used two alternative phylogenies for the analyses. In the main text, results of analyses conducted obtaining a phylogeny for Columbiformes from the bird tree project (Jetz et al. 2012) encompassing 304 species of pigeons and doves. Parallel, we confirmed the results using the phylogeny implemented in Lapiedra et al (2013) encompassing 154 species. A random sample of 100 trees was stored and used in all subsequent analyses. This allows taking into account phylogenetic uncertainty of the tree topology as the reversible jump model samples different possible topologies and branch lengths as a function of their posterior probabilities, providing a more reliable phylogenetic framework to conduct the analyses.

Relationship between morphological and ecological variables

To model variation in tarsus length as the result of geographical, ecological and behavioral variables, we used a Phylogenetic Generalized Least Squares approach (PGLS) using the R package “caper” developed by Orme (2012). This method allows quantifying the relationship among discrete ecological and continuous morphological variables while simultaneously controlling for the non-independence of data due to common ancestry. This is done by incorporating the phylogenetic variance-covariance matrix in the model. Morphological data came from a phylogenetic PCA (Revell 2009) computed from the log-transformed values of the morphological variables to define the shape of species in a multi-dimensional space to be used in the PGLS analyses while accounting for the non-independence among them due to shared phylogenetic history. Species-level variables tested in the analysis included two components of the geographic envelope (continent Vs island) and the maximum distance from the equator of the species distribution, habitat type simplified to separate forest-dwelling species from those living in open areas, the foraging behavior quantified as the degree of arboreality and diet type quantified as the degree of frugivory.

Phylogenetic morphospace, reconstruction of variables and evolutionary transitions in the phylogenies

We conducted phylogenetic morphospace representations (Revell 2012) to represent graphically the degree of morphological segregation associated with phylogenetic relatedness, geographic isolation, macro-habitat and micro-habitat factors. To reconstruct the history of such factors in the evolutionary history of Columbiformes, we used stochastic character mapping (Huelsenbeck et al. 2003), a Bayesian method that applies a Monte Carlo algorithm to sample the posterior probability distribution of ancestral states and timings of transitions on phylogenetic branches under a Markov process of evolution (Huelsenbeck et al. 2003). The R package "phytools" (Revell 2012) was used to build stochastic character-mapped reconstructions as detailed elsewhere (Lapiedra et al. 2013). The "simmap" formatted trees obtained were used in the analyses as a way of taking into account the uncertainty associated to phylogenetic hypotheses and the reconstruction of ancestral states. Species were grouped into categories encompassing whether they usually use a terrestrial or an arboreal foraging strategy, whether they inhabit open areas or forests and if they live in continents or islands. Groups with less than ten species were excluded because from the analyses. Thus, the categories are as follows: all species inhabiting open areas were pooled in a single category - terrestrial species inhabiting open areas in continents; "TOC" hereafter. Then, species inhabiting forests were divided into four categories: "TFC" referred to terrestrial, forest-dwelling species inhabiting continents and those living in islands –"TFI"-. Finally, all arboreal species inhabit forested areas. They are divided into two groups depending on whether they live in continents -"AFC"- or in islands –"AFI"-.

Information of evolutionary transitions was obtained from these reconstructions and used to study how such transitions have occurred along the clade's evolutionary history. These results were summarized using the "describe.simmap" function in "phytools" (Revell 2012) applied to a file including 1000 evolutionary reconstructions. This allowed us to show that some evolutionary transitions are restricted and to show how the evolutionary path followed by ancestral Columbiformes seems to follow an ordered sequence of changes.

Model selection for morphological evolution

Seven different models of character evolution were fitted to data describing the evolution of relative tarsus length in Columbiformes using the R package OUwie (Beaulieu et al. 2012). Our aim was to identify whether and how different combinations of the traits identified in the PGLS analysis play a role in such evolutionary process. Detailed information on the models can be found elsewhere (Beaulieu et al. 2012). Based on our hypotheses and previous results (Lapiedra et al. 2013) we predicted that some of the combinations of geographic, ecological and behavioural traits may evolve around different phenotypic optima. This hypothesis can be tested by fitting Ornstein-Uhlenbeck models (OU hereafter) that can model selective constraints associated with different trait combinations. Five OU models were applied to morphological data. Such models differ in how their rate parameters are allowed to vary. Three parameters can vary among groups: phenotypic optima, strength of selection (rate of evolutionary change), and the rate of stochastic variation around the optima (2012). The idea is as follows. For example, it could be that terrestrial, forest-dwelling species inhabiting islands had a different phenotypic optimum than those inhabiting continents (optima may differ). It may also happen that the strength with which natural selection pulled phenotypes toward such new optima was more strong in islands (higher alpha score), or that less phenotypic variation around the new optima existed due to some sort of evolutionary constraints (e.g. the phenotype needed for terrestrial, forest-dwelling lineages to thrive in islands may be very specific). The simplest model was an OU model with a single optimum and the same rates of evolution and variation around the optimum applied to all branches, independently of their behavioural state (‘OU1’ model). The other four OU models differ in how they allow the parameters to vary but not others. OUM is a model with different phenotypic optima and identical strengths of selection and rate of stochastic motion around the optima on all selective regimes. OUMA model also allows the strength of selection to vary among selective regimes while the OUMA model alternatively allows the rates of stochastic evolution away from the optimum to vary, but not the strength of selection. Finally, the OUMVA is the complete model where all three parameters can differ among groups. Alternatively, it could be that no different phenotypic optima existed among groups. We tested such possibility by fitting two Brownian motion (BM hereafter). BMS is a model where different rates of evolutionary change may exist while BM1 represents a model with no differences among groups. Results from 100 different trees were integrated and, following Lapiedra et al. (2013), we used a model-averaging approach, where we calculated the Akaike weights for each model (i.e. the relative likelihood of each model) by means of the second-order Akaike information criteria (AICc). The parameter estimates for each model were then averaged together, using their corresponding Akaike weight (AICw) as the weights.

Species-level lineage diversification rates

It is the inverse of the Equal Splits (ES) measure of evolutionary isolation (Redding & Mooers 2006) as estimated by Jetz and collaborators (2012). This is a measure of the splitting rate of the path to a tip: species in rapidly-diversifying clades will have short edge lengths shared among many species and low ES values, while isolated species on a tree have no evidence of recent diversification and large ES values. We used this measure to identify if the scores of DR varies across regions and / or ecological categories (again by means of a PGLS approach using the "caper" package (Orme 2012)). This measure is possible because we have now the full resolution of the phylogeny of the group (Jetz et al. 2012).

Results

Morphological predictors

The relationship between the hindlimb morphology and behavioral, geographic and ecological predictors was complex. The single best model identified by a model selection approach was highly consistent across 100 phylogenies randomly drawn from the posterior distribution and included a triple interaction between foraging strategy, insularity and habitat type (Table 1). The triple interaction firstly suggests that ground-dwelling species have generally longer tarsi than arboreal species (Table 2; Figure 1), confirming previous results, but that this difference is more accentuated in forest-dwelling species than in species primarily occurring in open habitats. This pattern is replicated in species inhabiting continents as well as for lineages inhabiting islands and is also replicated in two of the three main clades (i.e. clades "A" and "C") in which *Columbiformes* have been subdivided (the last clade, "clade B", does not have any arboreal species).

Secondly, the effect of habitat in the interaction arises from the fact that species inhabiting open areas, all of which exhibit a terrestrial foraging strategy, had shorter tarsi compared to terrestrial species from forests (Table 2). A more detailed analysis of the pattern revealed that this was mainly due to the effect of species from clade B, which had much shorter tarsi than the terrestrial species from other clades (Figure 1 Supplementary Material).

Finally, the interaction also results from the fact that terrestrial species inhabiting islands tended to have longer tarsi than their continental counterparts. Such differences are mainly the consequence of island-dwelling species from clade “C” (Figure 1; p-value = 0.017) while this difference did not exist among terrestrial lineages within clade A (p-value 0.955). Parallel, this pattern was repeated for arboreal species in clade “C” (p = 0.028) while it did not occur for species in clade “A” (p = 0.305) (Figure 1 Supplementary material).

Evolutionary transitions

The analysis of evolutionary transitions revealed a sequence in the geographic, ecological and behavioral changes that lead to the evolution of tarsus length in pigeons and doves. Provided that the ancestor of Columbiformes was “TOC” or “TFC”, transitions showed that terrestrial-dwelling lineages colonized islands before shifting to an arboreal foraging strategy (Table 3; Figure 2) and this was replicated several independent times. This is, only terrestrial species inhabiting forests in islands evolved to an arboreal foraging strategy (Table 3). Also, confirming previous results (Lapiedra et al. 2013), no transitions occurred from arboreal to terrestrial foraging strategy (Table 3) although more than half the extant species of Columbiformes have an arboreal foraging strategy. The median number of transitions among categories estimated from 1000 different trees is 66 (Table 3; Figure 2 Supplementary). From these, 33 transitions (50 %) corresponded to a single bi-directional path: transitions of arboreal species re-colonizing continents (median of 20 transitions) or arboreal continental species colonizing islands (median of 13) suggesting that transitions among arboreal lineages are much more frequent than the rest of transitions. On the other hand, most transitions to TFI came from TFC (median of seven) rather than from TOC (median of two transitions). Note that a transition from TOC to TFI implied two simultaneous changes at a time (invading a forested area and colonizing an island).

Evolutionary models

An OU model with different phenotypic optima, different evolutionary rates, and different degrees of variation around the optima (OUMVA) was the model that best fitted the evolution of tarsus length in Columbiformes (Table 4a). A number of patterns were revealed from this analysis. First, as predicted by results from the PGLS analysis, terrestrial lineages have longer tarsi than arboreal lineages. However, there is an exception. Terrestrial species inhabiting open areas "TOC" seem to be more similar to arboreal lineages. As stated above, this seems to be because of the influence of those terrestrial species inhabiting open areas from clade "B". Such species have tarsi that are much short than those of terrestrial forest-dwelling "TFC" species from the same clade. This pattern was not replicated in both clades "A" and "C", where terrestrial species inhabiting open areas have tarsi with a similar length than those lineages inhabiting forested habitats. Another difference in the phenotypic optima was that both terrestrial and arboreal species inhabiting forested areas in islands had longer tarsi than their mainland counterparts (Table 4b).

We predicted that the colonization of islands should enhance evolutionary change through a stronger pull by natural selection towards new phenotypic optima. This was confirmed by the models. After colonizing islands, the strength of selection pulling species towards a new phenotypic optimum was higher than for transitions occurring in continents (AFI = 0.092 +/- 0.01 compared with AFC = 0.73 +/- 0.02; and TFI = 0.95 +/- 0.01 compared with TFC = 0.052 +/- 0.01; Table 4b). On the other hand, we found that variation around the phenotypic optima was much higher among TOC species compared with all the rest of the groups.

We predicted that a shift in the foraging strategy may spur evolutionary change. Consistent with previous results (Lapiedra et al. 2013) we found evidence for this as alpha scores were higher in arboreal lineages for AFC compared with TFC (0.073 +/- 0.02 Vs 0.052 +/+ 0.01; Table 4b). However, this is not replicated in the case of AFI compared with TFI (Table 4b). Note that the strength of selection for TOC lineages was also low (TOC = 0.043 +/- 0.01).

To understand the consequences of the changes to arboreal behavior in terms of taxonomic diversification, we calculated the longer-term splitting rate leading to a given species. The analysis of this metric showed that speciation rates were not higher in island-dwelling species compared with continental species ($p > 0.05$). However, we found that the shift from terrestrial to arboreal behavior has brought associated an increase in diversification rate (speciation rates in arboreal foragers pooled together were higher than those of terrestrial foragers; $p < 0.05$; Figure 3). Interestingly, the subsequent colonizations of the mainland have not altered the rates of diversification. These results can reflect the high frequency of transitions between island-mainland and mainland-island, which may have favored reproductive isolation.

Discussion

Transitions from terrestrial to arboreal behaviors have rarely occurred during the evolutionary history of Columbiformes. This is to be expected because such transitions require moving between quite different adaptive peaks, as reflected by the estimated optima for hindlimbs in terrestrial and arboreal Columbiformes (Figure 2; Table 4b).

More importantly, transitions from terrestrial to arboreal behaviors have exclusively occurred on islands. This has occurred several independent times along the evolutionary history of the group (for example, it has occurred in different clades sense Pereira et al. (2007)). This is remarkable because despite that islands are often assumed to favor evolution as a result of reduced dispersal, limited gene flow and increased ecological opportunity (Stuart et al. 2012), there is little evidence for this to be the case. We believe such shifts are more likely on islands because island tend to contain less enemies and competitors and have clear barriers that limit dispersal. Theory suggests that such scenarios can favor niche expansion within populations (Van Valen (1965)). Populations can also more easily reach their carrying capacity and increase intra-specific competition. This can lead some individuals to shift to use alternative resources as has been reported in experimental studies (Svanback & Bolnick 2007). This was also found in zenaida doves (*Zenaida aurita*) from Barbados islands. In this species, individuals either aggressively defend feeding territories from conspecifics or feed in large unaggressive groups with conspecifics. This resource polymorphism appears to primarily result from competition for territories, which forces less competitive individuals to use alternative, suboptimal resources (Sol et al. 2005c).

We have reported that behavioral changes in foraging mode have brought associated changes in hindlimb morphology. However, we found no evidence that the entrance into this new adaptive zone has enhanced morphological disparity. This has not been the only evolutionary consequence of shifts in foraging behavior in pigeons and doves. They have also led to increased speciation rates when lineages have acquired an arboreal behavior. We have rejected that this has to do exclusively with reproductive isolation, as terrestrial species inhabiting islands do not show such acceleration. Arboreal species may have higher dispersal abilities. This is supported by the much higher number of island-mainland transitions in arboreal compared to terrestrial species. Although this should be studied further, we suggest that one cause may be that they differ n their ecology. Particularly, numerous tropical and subtropical arboreal-dwelling species show a nomadic behavior when they search for fruiting trees and they are even seen quite frequently in islands where they do not breed (Gibbs et al. 2001).

Some authors have suggested that there may be a general sequential pattern in the evolutionary development of the ecological niche of species (Todd Streelman & Danley 2003; Pearman et al. 2008; Gavrilets & Losos 2009), with divergence with respect to habitat preceding the evolution of microhabitat choice (e.g. foraging strategy). Pigeons seem to have followed such a sequence, with factors that promote speciation preceding the ecological shifts that facilitate adaptive change. Allopatric speciation is the main mode of diversification in birds (Price 2008). Once a population has speciated, gene flow is interrupted and this facilitates local adaptation. Evolutionary divergence can also be enhanced if the new species and its ancestor enter in contact again, as then competition between them should lead to character displacement (the divergence in traits associated to resource use; (Ricklefs 2004). The consequence will be a rapid evolutionary divergence in traits or attributes associated with the use of different resources. Other sequences of changes have been reported in the niche evolution of some other birds, such as Darwin finches (Grant & Grant 2002) and warblers of the genus *Phylloscopus* from the Himalayas (Richman & Price 1992). Darwin (1859) was the first to suggest that ecological divergence is an important motor of evolutionary diversification. In *On the Origin of Species*, he used feral pigeons to provide evidence for the evolutionary force of natural selection. Yet this conclusion was based on artificial selection experiments rather than on observations of nature. Our findings highlight the importance of integrating different dimensions into the study of a clade’s evolutionary diversification and contribute to the confirmation of the ecological theory of evolution, the idea that evolutionary diversification results in part from divergent selection on populations exposed to contrasting environments (Schluter 2001). Our results confirm the existence of such a sequence in geographic range expansions (in this case, the colonization of islands) precedes behavioral modifications (a shift to an arboreal foraging strategy) that have driven phenotypic evolution.

The most likely evolutionary scenario for the diversification of the ecological niche of pigeons is as follows. The ancestral state of all pigeons and doves was terrestrial and inhabited continental land (either TOC or TFC; see Supplementary Table S2). Eventually, some of these ancestors colonized islands (TFI). This happened a few times. Although such transition was possible following both paths from TOC and TFC, however, they exclusively occurred from TFC (median of seven transitions) rather than from TOC (median of two transitions; Table 3; Figure 2 Supplementary). TFC species colonizing islands tended to increase tarsus length (mean increase in phenotypic optimum = + 0.133). The same happened for TOC becoming TFC (+ 0.213). Other transitions have occurred a number of times reverting these changes from TFI species re-colonizing continents (TFI → TFC, median of five transitions) and, less frequently, re-colonizing open areas in continents (TFI → TOC, median of a single transition). After such geographical range expansion, some terrestrial, forest-dwelling island lineages shifted to an arboreal foraging strategy (TFI → AFI). Such behavioral niche shift was crucial for two reasons. First, it drove the largest change in the phenotypic optimum of such lineages (Figure 2 Supplementary) confirming that shifts in the foraging strategy are capital for tarsus length evolution (Lapiedra et al. 2013). Such change was towards much shorter tarsi in arboreal lineages (- 0.500). Second, this shift allowed pigeons and doves to become arboreal specialists for the first time, which has allowed for a subsequent remarkable species diversification. In fact, more than half of the extant Columbiformes species are arboreal specialists derived from these transitions. Such new phenotypic optimum for arboreal species was maintained in subsequent re-colonizations of continental areas by arboreal species (AFI → AFC). Importantly, this island-colonization-continent-re-colonization loop has been much more frequent than any other transition (it represents 50 % of all transitions; see Figure 2 Supplementary). Thus, this is likely to have facilitated multiple reproductive isolation events in allopatry, facilitating speciation events that lead to the current large diversity of arboreal-dwelling species.

Evidence that range expansions represent the starting point for the adaptive diversification of the lineage are consistent with the idea that changes in the distribution of species may facilitate reproductive isolation and at the same time exposes populations to new environmental conditions to which they subsequently tend to adapt to. In fact, Phillimore et al. (2006b) identified dispersal ability as the most important ecological trait associated to species' diversification in birds. When birds arrive to new areas, novel selective pressures may force them to move into alternative habitats. Subsequently, because of the novel distribution of resources or due to interspecific competition, they may eventually shift their foraging behavior, which spurs morphological evolution associated with divergent natural selection. In the case of arboreal-dwelling pigeons, this may be related with the ecology of many tropical and subtropical species, which are predicted to have high dispersal abilities (Pereira et al. 2007) associated with their nomadic behavior in search of fruiting trees which usually leads them to fly over the ocean (Gibbs, D., Barnes, E., Cox, J. 2001).

Altogether, we show that ecological opportunity associated with the colonization of islands together with the acquisition of an arboreal foraging strategy have been crucial in allowing the phenotypic differentiation of derived pigeons and doves. However, we reject the hypothesis that island colonizers experienced an ecological release –both for terrestrial and arboreal lineages- because within-group tarsus length variation is limited. Thus, we conclude that the colonization of islands paved the way for a behavioral change to occur, which allowed pigeons and doves to invade a novel major ecological niche: the arboreal foraging niche. Indeed, the acquisition of an arboreal foraging strategy may be considered as a key innovation in Columbiformes. However, although changes in the foraging strategy have been crucial for adaptive diversification, range expansions in the form of island colonizations and continental re-colonizations are the main reason explaining the current high diversity of arboreal-dwelling species.

Conclusions

Most past evolutionary thinking has assumed that evolution is primarily governed by extrinsic forces, like environmental changes or ecological opportunities. However, by changing their behavior animals are able to shape the selective pressures that affect them, and hence intrinsic forces can also be important in driving evolution. Indeed, the behavioral drive hypothesis fits well with the so-called ecological theory of speciation (Schluter 1998; Losos 2010), which states that much of current diversity is the results of selection acting on individuals using different habitats or resources. Based on a comparative analysis of all species within a major evolutionary radiation in birds, we show here that behavior may drive evolutionary diversification by modifying the way individuals interact with their environment. However, our results also highlight that its evolutionary consequences largely depend on the limits imposed by the functional demands of the adaptive zone. Thus, both intrinsic and extrinsic forces seem critical to explain the evolutionary diversification of animals and should be integrated in studies investigating with the causes of animal evolutionary diversification.

Table 1: Results from a PGLS of the evolution of hind limb length including geographic, ecological and behavioral factors following Orme et al (2012)

Trait	Variable	Estimate	SE	t-value	P
PC2	(Intercept)	-0.0115	0.226	-0.0509	0.9595
	Foraging	0.2412	0.150	1.6103	0.1095
	Habitat	0.0881	0.050	1.7585	0.0808
	Insularity	-0.0040	0.165	-0.0246	0.9804
	Forag.Strategy*Habitat	-0.4481	0.155	-2.8936	0.0044
	Forag.Strategy*Insularity	6.0444	2.168	2.7877	0.0060
	Habitat*Insularity	0.1149	0.181	0.6360	0.5258
	Forag.Strategy*Habitat*Insularity	-6.1284	2.173	-2.820	0.0055

Table 2: Post-hoc analysis derived from a phylogenetic ANOVA analysis of the differences between tarsus lengths in different groups following Revell (2012)

	AFC	AFI	TFC	TFI	TOC
AFC	-	0.230	0.004	0.001	0.935
AFI		-	0.078	0.008	0.390
TFC			-	0.320	0.001
TFI				-	0.001

Table 3: Evolutionary transitions in 1000 trees computed with “phytools” (Revell 2012)

		To				
From		TFC	TOC	TFI	AFI	AFC
TFC	Mean		9.09	7.34	0.12	0.11
	Sd		2.41	2.39	0.44	0.67
	Median		9	7	0	0
	95 % CI		8.94-9.24	7.19-7.49	0.10-0.15	0.07-0.15
TOC	Mean	7.15		1.72	0.16	0.12
	Sd	2.65		0.97	0.44	0.46
	Median	7		2	0	0
	95 % CI	6.98-7.31		1.66-1.78	0.13-0.19	0.09-0.15
TFI	Mean	5.08	1.59		1.71	0
	sd	2.47	1.09		1.12	0
	median	5	1		2	0
	95 % CI	4.92-5.23	1.52-1.65		1.64-1.78	0.00-0.00
AFI	Mean	0.2	0.08	0.22		20.21
	sd	0.52	0.31	0.51		4.22
	median	0	0	0		20
	95 % CI	0.17-0.23	006-0.10	0.18-0.25		19.95-20.47
AFC	Mean	0.16	0.12	0	13.37	
	sd	0.98	0.75	0.03	4.23	
	median	0	0	0	13	
	95 % CI	0.10-0.22	0.07-0.16	0.00-0.00	13.10-13.63	

Table 4: Table 4a shows the mean scores for the models of morphological evolution applied to the evolution of tarsus length in pigeons and doves from 100 different trees. Table 4b shows the mean parameter estimations for the best model estimated (in all cases the best model is an OUMVA)

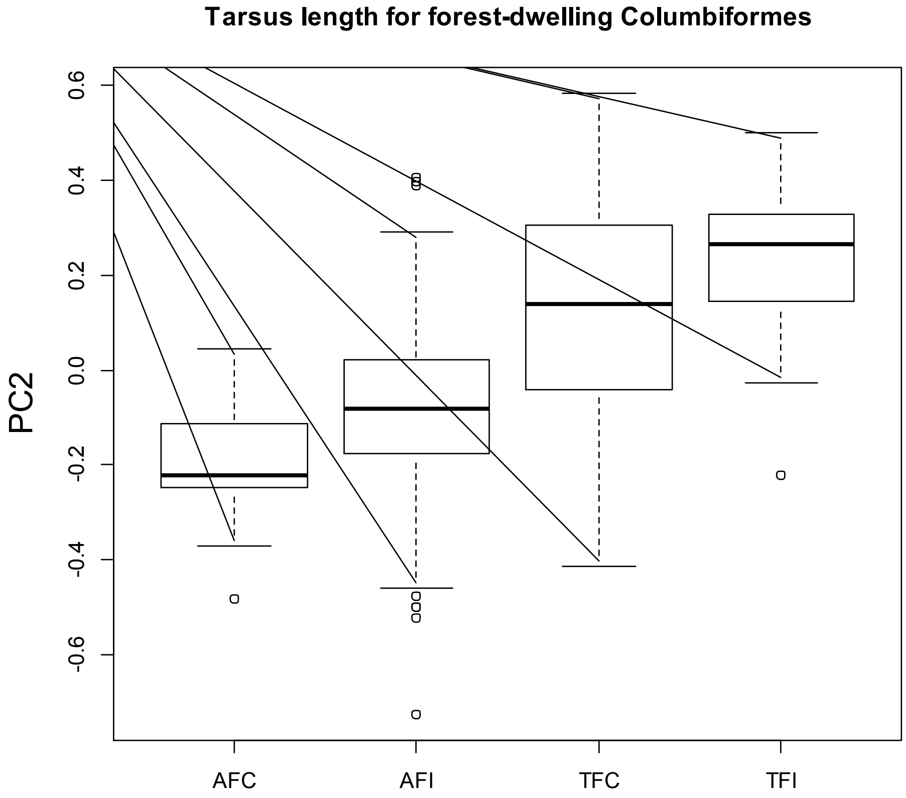
4a)

Models	BM1	BMS	OU1	OUM	OUMV	OUMA	**OUMVA**
Mean AICc	-59.94	-83.81	-117.43	-165.73	-176.34	-171.66	**-192.51**

4b)

	θ_AFI	**θ_TFC**	**θ_TFI**	**θ_TOC**	**θ_AFC**
Mean	-0.1009	0.1682	0.2549	-0.2543	-0.2689
SD	0.0364	0.0364	0.0289	0.1916	0.0829
SE	0.0038	0.0038	0.0030	0.0156	0.0085
	α_AFI	**α_TFC**	**α_TFI**	**α_TOC**	**α_AFC**
Mean	0.0834	0.0596	0.0811	0.0544	0.0734
SD	0.0312	0.0237	0.0292	0.0226	0.0297
SE	0.0032	0.0024	0.0030	0.0023	0.0031
	σ²_AFI	**σ²_TFC**	**σ²_TFI**	**σ²_TOC**	**σ²_AFC**
Mean	0.0039	0.0033	0.0031	0.0159	0.0052
SD	0.0012	0.0015	0.0022	0.0093	0.0057
SE	0.0001	0.0002	0.0002	0.0010	0.0006

Figure 1: Tarsus length variation depending on the geographic, ecological and behavioral categories investigated



�ri : Pa�0I��-ò0AcJòM�gE�cg�MDJcJòMD��3 òMr �1�cer ògJeD�1ò3 �JM.Mr �r eòr g�: , J1�9JD0�MB�6�3 �JM0�MB�8�5� , ��Jc�c�cE: e�9tògeDcD�� D�ò: eM��ge�D8��MB��e, �-Jòg�09ceggeDcgJ�06�� D��g�òge�06BC e00Mr 8� BJ3 eMDJòMD�òt�c, e�M1, ek���ceD�òt�cg�MDJcJòMD��ge�ge: geDeMceB��E�c, e�C JBc, �òt�c, e��ggòC D�JM� : gò: ògcJòM�cò�c, eJg�tgePAeM1E��eDcJ3 �ceB�tgò3 ���D�3 : 0e�òt�úNNN�DJ3 3 �: 6tòg3 �cceB�cgeeDk� � e�M�D1ògeD�JM�c, e�3 e�M� , eMòcE: J1�ò: cJ3 ��1, �Mr eD��ecC eeM�cg�MDJcJòMD��3 òMr �1�cer ògJeD� �ge�JMBJ1�ceB�JM��0�12�9: òDJcJ-e�D1ògeD�3 e�M�JM1ge�De�JM�c, e�c�gDAD�0eMr c, ��MB�Mer �cJ-e�D1ògeD� 1ògge D: òMB�cò�1, �Mr eD�còC �gB�D, ògceg�, JMB�03 �Dk��McJ�0D�Dc�MB�tòg�c, e�tòg�r JMr �3 òBe� 9�] ceggeDcgJ�05��] �g�òge�085�, ��Jc�c�cE: e�9�] tògeDcD5��] ò: eM��ge�D8��MB�JMDA0�gJcE�9�] D: e1JeD� 0-JMr �JM�1òMcJMeMcD��MB��] JD0�MBD8k�

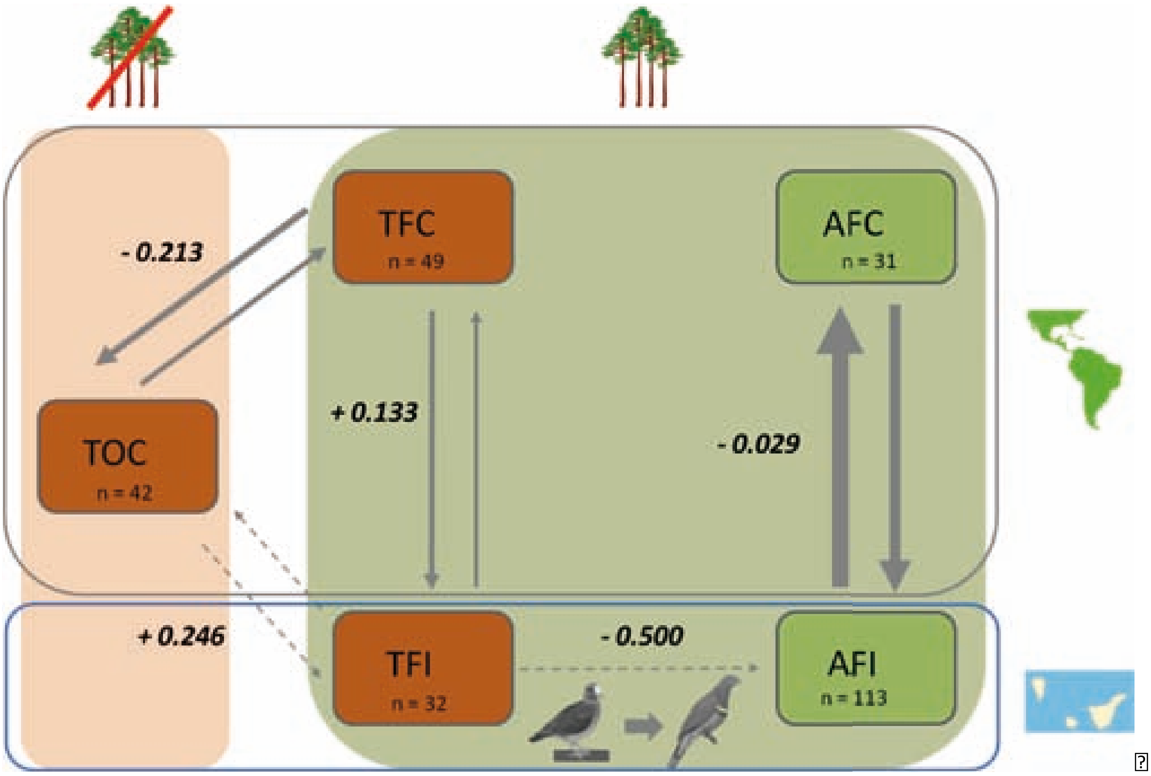
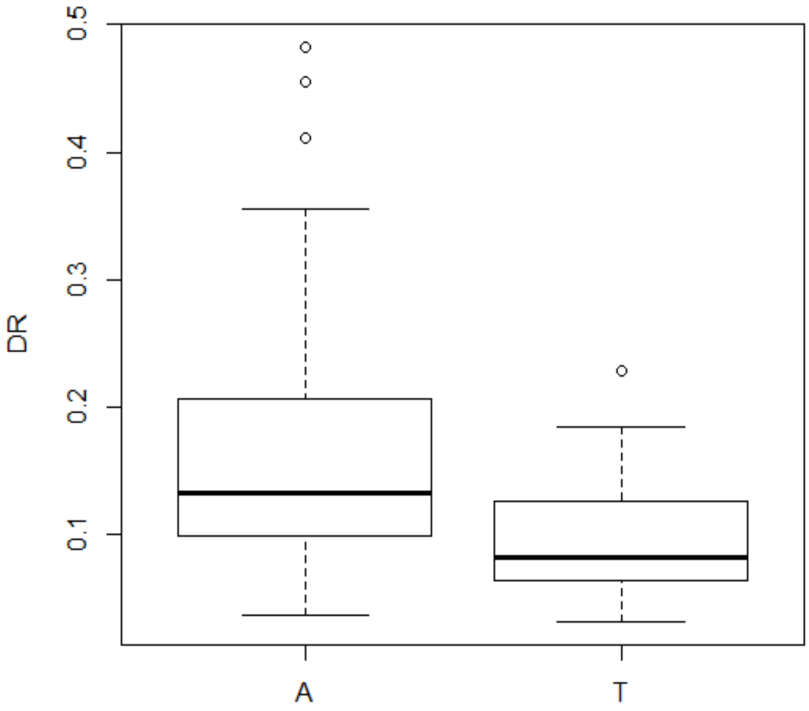


Figure 3: DR estimates computed from splitting rates following Jetz et al. (2012)

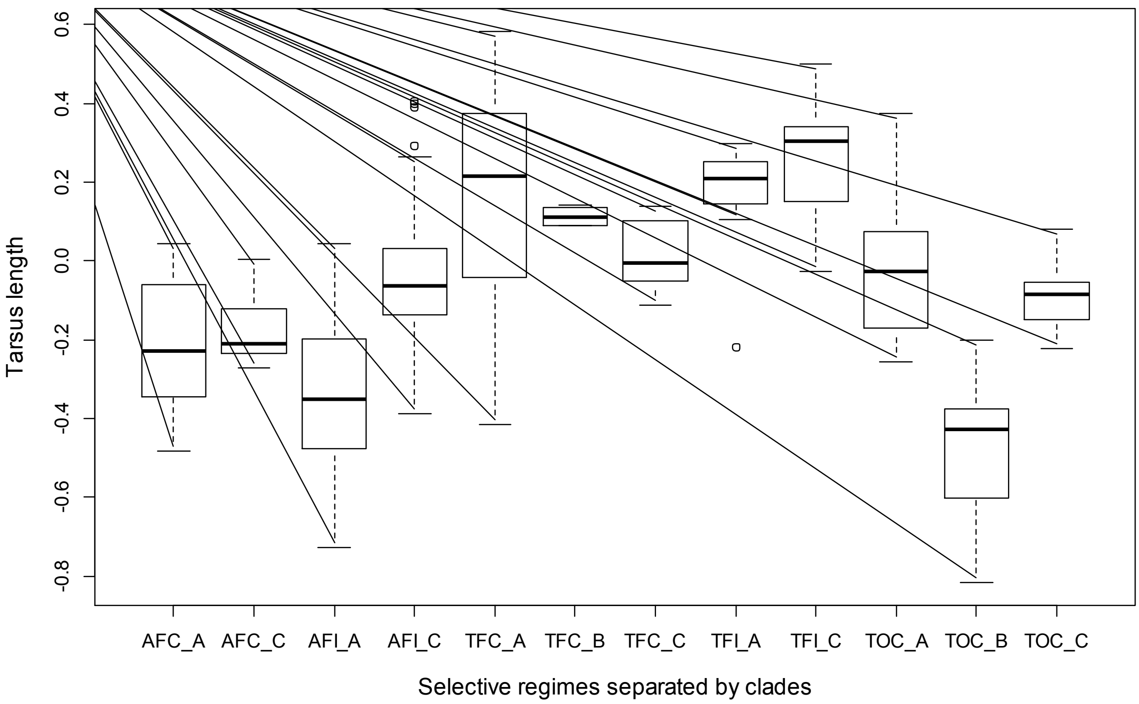


Supplementary material

Table S1: Phylogenetic PCA components

	PC1	PC2	PC3	PC4
% explained	67.75	17.15	11.26	4.03
eigenvectors				
wing	-0.307	-0.034	0.067	0.949
tail	-0.855	-0.082	-0.447	-0.248
tarsus	-0.087	0.996	-0.021	0.009
beak	-0.408	-0.015	0.891	-0.196

Figure 1: Tarsus length variation depending on the geographic, ecological and behavioral categories investigated and grouped for every clade (sensu Pereira et al. (2007)



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Chapter 4

A framework for estimating niche metrics using the resemblance between qualitative resources [3]

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[3] With Miquel de Cáceres, Daniel Sol and Pierre Legendre. **Oikos**; 120:9 (1341–1350), September 2011

Abstract

Despite the central importance of the niche concept for the ecological theory, current methods to quantify the species niche from qualitative resources, such as food or habitat types, remain insufficiently developed. Classically, information theory and diversity measures have formed the toolbox used for calculating resource niche metrics on species preference data for a set of qualitative resources. We provide a comprehensive framework that extends these classical approaches by incorporating the resemblance between resources into the calculation of resource niche metrics. This does not only allow estimation of the niche centre, breadth, overlap and displacement with greater accuracy, but also makes the estimates less influenced by the way the resources are subdivided. In addition, all niche metrics can be calculated while taking into account the variation in resource availability, and confidence intervals can be obtained by bootstrapping. We illustrate the utility of the framework with an analysis of dietary preferences in feral pigeons (*Columba livia*).

Keywords: diversity measures, niche breadth, niche overlap, Rao’s entropy, principal coordinate analysis.

Introduction

The fundamental ecological niche of a species is the set of ecological requirements individuals need for survival in the absence of competition, predation, dispersal limitation, and natural or human disturbances (Hutchinson 1957). Thus, the niche concept underlies most ecological questions, from population growth and geographic expansion to community dynamics and ecosystem functioning (Austin and Smith 1989, Owens and Bennett 2000, Chase and Leibold 2003, Phillimore et al. 2006). Since the development of niche theory by MacArthur and his collaborators (summarized in Vandermeer 1972), field ecologists have been interested in measuring the niche of species. However, the fundamental niche of a species is usually impossible to quantify, and at the most we can try to measure the part of the fundamental niche actually occupied by the species after the constrains above-mentioned, the so-called realized niche (Hutchinson 1957, Pulliam 2000). The past decades have seen a proliferation of methods to quantify the realized niche of species based on quantitative environmental factors, such as climatic or soil variables (e.g. Peterson et al. 1999, Thuiller et al. 2004, Calenge and Basille 2008). In contrast, considerable less effort has been devoted to develop methods to estimate the niche defined as the preference for a set of qualitative resources (e.g. food types) required for survival and reproduction. Describing an operational method to measure the qualitative resource niche of organisms is the goal of the present paper.

Information theory and diversity measures have traditionally conformed the toolbox used for calculating qualitative resource niche metrics in the past (e.g.Horn 1966, Colwell and Futuyma 1971, Hanski 1978, Hurlbert 1978, Gordon and Illius 1989, Mysterud 2000, Blüthgen et al. 2006). These metrics may be calculated from measures of the observed use or preference for the resources (e.g. the fraction of each prey consumed). Unfortunately, most of traditional measures do not take into account the fact that some resources may be more similar than others, and hence all resources are treated as equally distinct (Colwell and Futuyma 1971). Not taking into account unequal resource resemblance is problematic, because niche metrics are sensitive to how resource categories are defined and weighted. For example, dividing a given resource into two similar subcategories can artificially inflate niche breadth because a species preferring the initial resource will also show high preference for the two subcategories. Such biases can only be prevented if resource distinctness is incorporated into the niche breadth measure. Colwell and Futuyma (1971) were the first to propose niche metrics that accommodated resource distinctness. However, their approach only allowed to estimate niche breadth and overlap, and was deemed difficult to interpret by some (Hanski 1978). Later developments of resource niche metrics did not further extend these novel ideas but instead concentrated on solving another limitation, that is, the incorporation of variation of resource availability in the metrics (Hurlbert 1978, Lawlor 1980, Feinsinger et al. 1981, Smith 1982).

The framework we describe in the present paper revisits and generalizes Colwell and Futuyma (1971) ideas in an attempt to produce niche metrics that are more accurate and less affected by the way the different resources are defined. Like their approach, our method incorporates the resemblance between resources into the calculation of resource niche metrics. Unlike their approach, ours is more general, making it possible to estimate of a large number of niche metrics, and it allows the graphical representation of all these niche metrics on the resource space. The framework also allows incorporating the variation in resource availability in the computation of resource metrics, for the cases where this is deemed necessary, and it may be implemented at different ecological levels (including individuals, populations, species and communities) and within different temporal and spatial scales (Bolnick et al 2003, De Victor et al. 2009).

The greatest difficulty of our framework is to estimate the degree of distinctness of resources to be incorporated in the niche metrics. Colwell and Futuyma (1971) argued that this may be assessed based on the own information on resource preferences. However, computing resource distinctness in terms of the species perception has an element of circularity because preferences are used twice, first to quantify the distinctness between resources and then to estimate the niche parameters based on resource distinctness. A way to circumscribe this problem is to quantify the distinctness between resources based on features of the resource categories that are ecologically meaningful and relevant for the purpose of the study. For example, in a food sources analysis of a granivorous bird, like the one we present later on to illustrate the method, it may be appropriate to consider the size and hardness of the seeds as these attributes are known to affect foraging performance (Herrel et al. 2009).

In the following section, we describe the details of the proposed framework, and suggest a number of metrics useful to define the qualitative resource niche of organisms. We also cover the derivation of bootstrap confidence intervals for niche metric estimations. We then move to an example of application where we explore the trophic niche of feral pigeons (*Columba livia*). We finish by discussing the advantages and limitations of the suggested framework as well as the applications that we envision in the future. All the proposed methodological developments have been implemented in an R package called 'resniche', which is currently available from the first author's website[1].

The method of resource niche analysis

Resource use, availability and preference

Resource niche analyses are based on observations of species *resource use*. Let s be the number of species and r be the number of resources used by those species (e.g., food types, habitats or substrates). Resource use data is often in the form of an $s \times r$ table $\mathbf{U}$ where each u_{ij} value is a quantitative assessment of how much the species i is using the resource j (Fig. 1a). If resources are habitat types, a given u_{ij} value will typically be an assessment of the number of individuals, cover or biomass of the target species in habitat j. If resources are diet types, u_{ij} values will be assessments of food consumption, such as prey number, volume or mass (e.g. Griffiths 1986, Vitt and Pianka 2005). Now let $\mathbf{P}$ be the $s \times r$ table obtained after dividing each value u_{ij} by the sum of values of the corresponding row. Each p_{ij} value is hence a proportion expressing the *relative resource use* that species j makes of resource i.

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[1] http://sites.google.com/site/miqueldecaceres/

Resource use is not the same as resource preference, especially if resource availability differs within the area of study (Hurlbert 1978, Lawlor 1980, Feinsinger et al. 1981, Smith 1982). If a particular resource is relatively scarce it may represent only a small proportion of use, even if the species has a high preference for that resource. Conversely, some resources for which the species preference is low may be frequently used simply because they are abundant. Although in most real communities the distinction between resource use and preference will be difficult to make, we think that resource niche metrics should be computed on the basis of estimates of the species' resource preferences. Whether or not species resource use values can be taken as the species preference, is a question that should be tackled before computing niche metrics. Let **p** be relative resource use of a given target species (i.e. a given row of matrix **P**), and let **q** be a vector of resource availability values (i.e. q_i is the proportion of resource *i* available for use, Fig. 1b). When there is information on resource availability, species relative preference values can be calculated as:

$$f_j = \frac{p_j / q_j}{\sum_j^r p_j / q_j} \qquad (1)$$

If the distributions of the target species resource use and that of resource availability are equal, then the species has equal preference for all resources (Fig. 2a). If the target species uses resources in equal proportions but those are not equally available then the relative resource preferences are uneven (Fig. 2b). Finally, note that if resource availability data are not available or are not to be taken into account, then the relative species preference vector **f** is equal to the vector of relative resource use, that is $f_j = p_j$ for all resources.

The resource space

The key feature of our framework is the consideration of the geometric relationships between resources. These are described using an $r \times r$ distance table **D**, where each element d_{jk} contains the distance between the pair of resources *j* and *k* (Fig. 1c). The d_{jk} values may be obtained from relevant attributes of the resources considered. For example, for a dietary analysis one could use features such as prey size, nutritional content or even palatability or toxicity. Although **D** can be computed using any distance function, in order to facilitate the interpretation of some niche metrics we require that distance matrix **D** be Euclidean (Gower and Legendre 1986) and the distance values be bounded between zero (when the two resources are completely equivalent) and one (when the two resources are completely distinct). For those distance functions that do not produce Euclidean distance matrices (e.g. the Bray-Curtis and Gower distances), the **D** matrix can be made Euclidean by taking the square root of the d_{jk} values (Legendre and Legendre 1998, Table 7.2). If similarity values are available, one can easily transform them into distances. An advantage of having the distance relationships between resources is that one can display resource niches in an ordination diagram. To this aim, we suggest conducting a principal coordinate analysis (PCoA, Gower 1966) from table **D**. Using this procedure, we obtain a table **X** with r rows (resources) and m principal coordinate axes (where m is between 1 and r – 1) that represents the resource relationships in an Euclidean space. We will refer to these axes as the *resource space*. The species resource preferences can then be displayed in the resource space by using symbol sizes proportional to the resource preference value (Fig. 1e-f).

Resource niche metrics

In our framework one uses the resource space (i.e. either matrix **X** or, equivalently, matrix **D**) in the computation of resource niche metrics. In what follows, we use vector **f** as the resource preference of the target species niche. For niche metrics aimed at comparing two niche configurations, we will represent the two vectors of relative resource preferences by $\mathbf{f}_1$ and $\mathbf{f}_2$.

Niche centre – The centre of the species niche in the resource space is computed by averaging the coordinates of the resources preferred by the species, that is

$$\bar{x}_l = \sum_{j=1}^{r} f_j x_{jl} \tag{2}$$

where x_{jl} is the position of the jth resource on the lth axis of the resource space. If the species equally prefers all resources (i.e., if $f_j = 1/r$) then the niche centre will be at the overall centre of **X**.

Niche breadth – Early studies on niche analysis with qualitative resources measured the niche breadth with diversity measures, such as the Shannon-Wiener information index or the inverse of Simpson's concentration (Levins 1968, Colwell and Futuyma 1971, Hanski 1978, Griffiths 1986). In order to assess the niche breadth taking into account the relationships among resources, we suggest using Rao's quadratic entropy (Rao 1982), which is a general diversity measure that has been recently recommended to assess both functional and taxonomic diversity, and whose mathematical properties have been extensively studied (Shimatani 2001, Champely and Chessel 2002, Pavoine et al. 2005, Ricotta and Szeidl 2006, Ricotta and Marignani 2007). We chose the following notation for Rao's entropy:

$$B_D = \frac{1}{2}\sum_{j=1}^{r}\sum_{k=1}^{r} f_j f_k d_{jk}^2 \tag{3}$$

Eq. 3 has also been referred to as the Euclidean Diversity Coefficient (Champely and Chessel 2002). We can see that B_D can be interpreted as *half the average squared distance among the resources preferred by the target species*. An advantage of implementing Rao's entropy using eq. 3 is that it becomes equal to *the total variability among resources using the relative preference values as weights*:

$$B_D = \sum_{l=1}^{m}\left[\sum_{j=1}^{r} f_j \cdot (x_{jl} - \bar{x}_l)^2\right] \tag{4}$$

Therefore, the same quantity can be obtained using table **X** instead of **D**; The minimum niche breadth is 0; this value is obtained when all resources used are equal or when a single resource is used. For completely distinct resources (i.e., when the $d_{jk} = 1$ for $j \neq k$) B_D becomes the half the Gini-Simpson index (e.g. Pavoine et al. 2005):

$$B_D = \frac{1}{2}\cdot\left(1 - \sum_{j=1}^{r} f_j^2\right) \tag{5}$$

and the upper bound of B_D occurs for equal preference (i.e. $f = 1/r$). In general, however, the upper bound of B_D will depend on the resource distance values.

Distance between niche centres – The distance between niche centres is a simple and intuitive measure to compare the niche of two species, or to assess temporal displacements of the centre of a single species. This distance can be calculated from either **X** or **D** (Cuadras et al. 1997, Champely and Chessel 2002):

$$d_{12}^2 = \left\| \bar{\mathbf{x}}_1 - \bar{\mathbf{x}}_2 \right\|^2 \quad \text{(6a)}, \qquad d_{12}^2 = \sum_{j=1}^{r} \sum_{k=1}^{r} f_{1j} f_{2k} d_{jk}^2 - B_{D1} - B_{D2} \quad \text{(6b)}$$

Niche overlap – Resource niche overlap was defined in multiple ways in the past (Horn 1966, Schoener 1970, Colwell and Futuyma 1971, Pianka 1974, Sale 1974, Hurlbert 1978) and comparative studies exist (Ricklefs and Lau 1980, Linton et al. 1981, Mueller and Altenberg 1985). A measure that was frequently used was the cosine of the angle between the two vectors of relative resource preferences (Pianka 1974, Lawlor 1980, Rotenberry and Wiens 1980, Slobodchikoff and Schulz 1980):

$$O = \frac{\sum_{j=1}^{r} f_{1j} f_{2j}}{\sqrt{\sum_{j=1}^{r} f_{1j}^2 \cdot \sum_{j=1}^{r} f_{2j}^2}} \qquad (7)$$

which is symmetrical and ranges from 0 (no overlap) to 1 (complete overlap). We suggest here generalizing eq. 7 to take into account the resemblance between resources (see Appendix A.1.1):

$$O_D = \frac{\sum_{j=1}^{r} \sum_{k=1}^{r} f_{1j} f_{2k} (1 - d_{jk}^2)}{\sqrt{\sum_{j=1}^{r} \sum_{k=1}^{r} f_{1j} f_{1k} (1 - d_{jk}^2) \cdot \sum_{j=1}^{r} \sum_{k=1}^{r} f_{2j} f_{2k} (1 - d_{jk}^2)}} \qquad (8)$$

This index of overlap is also bounded between 0 (no overlap) to 1 (complete overlap). O_D will only yield zero overlap if the two vectors of preferences do not share any resource, and the resources preferred in one niche are completely distinct from the resources preferred in the other. This means that two species, one species preferring one resource only and the other preferring another resource, will still have some degree of niche overlap if the two resources have some similarity. Whenever the two vectors of preferences are equal, the overlap is always one regardless of the resemblance between resources.

Statistical inference on resource niche metrics

Niche metric estimates should be reported along with an indication of variance or a confidence interval (Fig. 1d). Studies have been published that develop analytical approximations to the variance of resource metrics (Smith 1982, Mueller and Altenberg 1985) or generate confidence intervals for estimates on the basis of re-sampling methods (Ricklefs and Lau 1980, Mueller and Altenberg 1985). All resource niche metrics presented here can be easily incorporated in the bootstrap framework described by Mueller and Altenberg (1985) and we will only briefly repeat it. An important point is that we consider the resource space (**D** or **X**) as fixed, whereas both the species resource use and resource availability are random variables. Suppose we obtained the estimates of relative resource use $\hat{\mathbf{p}}$ from a sample of size N_p. If each of the N_p observations is independent and identifies the use of a single resource (e.g. the species was observed once hunting that prey or in that habitat), then bootstrap samples $\hat{\mathbf{p}}^*$ can be generated by using a multinomial distribution with sample size N_p and probability values taken from the sample estimates. However, if target niche (e.g. for a population or a species) is described directly measuring **u** (or **p**) on several individuals (e.g. for every individual we assessed the proportions of food types from his stomachal content), then individuals are the units to be re-sampled with replacement. One pools the resource use vectors of re-sampled individuals in order to obtain $\hat{\mathbf{p}}^*$ for the bootstrap sample. Moreover, if relative resource availability estimates $\hat{\mathbf{q}}$ are available from a sample of size N_q, then bootstrap samples $\hat{\mathbf{q}}^*$ can also be generated using a multinomial distribution. Each pair $\hat{\mathbf{p}}^*$ and $\hat{\mathbf{q}}^*$ of bootstrap samples is then used to calculate the bootstrap estimate for species preference vector $\hat{\mathbf{f}}^*$ (eq. 1) and, assuming the resource relationships to be fixed, the bootstrap estimate for any resource niche metric. After generating many pairs of bootstrap samples one obtains a bootstrap distribution of the resource niche metric and calculates confidence intervals (Manly 1997).

Example: Diet preferences in two populations of feral pigeons (*Columba livia*)

We provide here an example of resource niche analysis where the main goal is to quantify differences in foraging niche breadth of feral pigeons based on diet preferences. To quantify diet preferences at an individual level, we used information from an ongoing food preference experiment. In brief, we captured free-ranging feral pigeons in two localities (Moià and Barcelona) from Catalonia (NE Spain), located 50 km apart. After capture, individuals were kept in outdoor aviaries for acclimatization during two weeks. Food consisted in a mixture of seeds, containing the six food types later used in the experiments. After acclimatization, birds were placed in individual cages and habituated for two days. The food choice experiment started after 18 hours of food-deprivation, when individuals were offered a six-section circular Plexiglas feeder containing 10g of six different seed types (green peas, oats, popcorn maize, soybeans, sunflower seeds, and wheat). Pigeons rarely consumed more than 10 grams of seeds during an experiment, which ensured that food consumption closely reflects food preferences of individuals. Individuals were allowed to feed for 20 minutes, after which we removed the feeder and measured the remaining amount of each food type with a digital precision balance. The quantity of each seed type consumed by each individual was estimated by subtracting this quantity from the initial 10g. All animal care, husbandry, and experimental procedures were in accordance with the Spanish code of practice for the care and use of animals for scientific purposes and were approved by the Generalitat de Catalunya (0152S, Dept de Medi Ambient i Habitatge).

We characterized the six seed types using descriptors of nutritional content (hydrocarbons, fats and proteins), as well as length and width (see Table 1a). These variables were standardized in order to remove differences due to units of measurement and the transformed variables were used to calculate the Euclidean (i.e.

Pythagorean) distance between pairs of seed types. We then divided the resulting distance matrix by its maximum value so as to obtain distances bounded between zero and one (Table 2). Popcorn, oats and wheat seeds were the most similar food types, solely differing in seed dimensions (Table 1a). In contrast, the maximum distance value was obtained between wheat and sunflower. Whereas wheat seeds are richer in carbohydrates than sunflower seeds, the latter are richer in proteins and especially fat. Moreover, sunflower seeds are much longer than wheat seeds (Table 1a). We studied diet resource niche at two ecological levels: individual and population.

Diet niche at the individual level – We calculated niche centres (eq. 2) and niche breadths (eq. 3 or 4) for each individual. Unfortunately, we did not have replicates of the experiment at the individual level, which prevented us from calculating confidence intervals for the different niche statistics. Individuals from the Barcelona population most usually ate wheat and sunflower seeds, with a lot of variability in the proportions. In contrast, individuals of the population in Moià ate either only wheat or combined with small amounts of other seed types, but generally avoided sunflower seeds (Fig. 3). Consequently, foraging niche should be broader for individuals of Barcelona than for individuals of Moià. This difference was significant when taking into account differences among seeds (Wilcoxon rank test, W = 328, p-value = 0.005) but not if seeds were considered equally distinct (W = 262, p-value = 0.2729). This result can be explained by the fact that the maximum distance occurred between sunflower and wheat seeds. Since Barcelona individuals ate mostly these two seed types, their niche breadths were quite similar regardless of resource distinctiveness. Those Moià pigeons that ate wheat and similar seeds, such as popcorn, had much narrower foraging niche estimates when resource distinctiveness was considered.

Diet niche at the population level – We assessed seed consumption at the population level by summing up the food consumptions of individuals belonging to each population (Table 1b). In this case, we could calculate bootstrap confidence intervals for niche metrics. We first calculated bootstrap estimates of seed consumption for a given population by re-sampling its individuals with replacement and summing up the food consumptions of the individuals in the sample. Bootstrap estimates of niche statistics were then computed using these bootstrapped seed consumption values. The preference values at the population level indicated the same differences in preference that appeared at the individual level (Table 1c): while in the Barcelona population seed preference is divided between wheat (45.5%) and sunflower (44.2%), in Moià population wheat seems to be the preferred diet source (79.1%). Consequently, the niche centre for the Barcelona population occurred midway between wheat and sunflower seeds, whereas that of Moià is very close to wheat (Fig. 3). Foraging niche was again broader for the Barcelona population than for the Moià population, and the difference appeared to be larger when resource distinctiveness was taken into account (Table 3). Finally, we found a substantial overlap (eq. 8) between the two populations sustained by the fact that both populations had a remarkable preference for wheat seeds. For the benefit of interested readers, we include in Appendix A.2 a small tutorial showing how the analyses with feral pigeons were conducted using R and the 'resniche' package.

Discussion

The niche concept is an important foundation for theories of ecological and evolutionary phenomena (Chase and Leibold 2003), but quantifying all the dimensions of the niche is operationally impossible. The alternative is to measure one or a few dimensions of the realized niche that are particularly relevant for the question being asked (Devictor et al. 2009). The framework that we propose to quantify the species resource niche goes in this direction. Our framework of resource niche analysis resembles the one proposed by Colwell and Futuyma (1971) in that resources are not assumed to be equally distinct, but their degree of distinctiveness is incorporated in the estimation of niche metrics. This has two main advantages. First, it allows researchers to obtain more accurate estimates of the resource niche of the species. The fact that some resources are more similar among them than when compared to others may lead to inaccurate estimates of the niche metrics if this unequal resemblance is ignored, entailing a loss of ecologically relevant information that may cause an underestimation of existing differences among studied organisms. Our analysis of pigeons' diet illustrates well this problem. There were niche breadth differences between populations, but these differences would not have been detected if we had not accounted for the distinctiveness between resources. The second advantage of taking into account resources distinctiveness comes when the investigator itself has to define the niche categories. The advantage is that the niche metrics become less influenced by the way resources are defined by the researcher (Abrams 1980). That is, if the researcher defines two resource categories that are found to be equivalent, then the two categories will lie in the same position of the resource space and our resource metrics (centre, breadth, overlap and displacement) will be unaffected (see Appendix A.1.2 and also Shimatani 2001).

While our approach resembles in important aspects that proposed by Colwell and Futuyma (1971), it also shows notable differences. First, it is more general, making it possible to estimate of a large number of niche metrics. In addition of niche breadth and overlap, one may estimate the niche centre and the distance to other niche centres. Second, the framework allows the graphical representation of all these niche metrics on the resource space. This may help address a number of ecological questions. For example, the resource space may be useful to track niche displacements in terms of both direction and intensity, a tool that may for instance be useful to study niche shifts during the ontogeny or to describe how resource partitioning changes across seasons or environmental conditions (Bolnick et al. 2002, Bolnick et al. 2003). We argued above that **D** should be a Euclidean distance matrix. If **D** is non-Euclidean, then negative eigenvalues will appear in the PCoA. In that case, one can still represent the real subspace of the relationships between resources in an ordination graph. The distance between niche centres can still be computed using the full resource space (Anderson 2006, Anderson et al. 2006), but negative niche displacements may occur. Incidentally, note that the resource niche can be complementarily studied using canonical ordinations, which allow relating the resource preference of species to a set of explanatory factors. For example, Vitt & Pianka (2005) used canonical correspondence analysis to show the relationships between diet and phylogeny in squamate reptiles. Finally, our framework makes it possible to estimate confidence intervals for all resource niche metrics presented here by using the bootstrap framework described by Mueller and Altenberg (1985). This allows consideration of uncertainty in niche size measurement.

While our approach may have broad applications in ecology and evolution, we think that it may be particularly useful in those areas where the resemblance between resources is expected to influence the results. One of these areas is the study of resource niche partitioning and individual specialization (Bolnick et al 2002; Bolnick et al 2003). Given that different organisms may have morphological (Herrel et al 2009), physiological and behavioural constrictions that limit their ability to exploit certain resources (Wenner & Sherry 1986; Bolnick et al 2003), not taking into account the resemblance between resources may cause an underestimation of the differences among studied organisms. Our analysis of the dietary niche of feral pigeons illustrates well this point. Another area we think can benefit from our approach is macroecology, where it is common to compare species with very distinct ecological requirements and where the resemblances between resources are unlikely to be equivalent. As highlighted by Chase and Leibold (2003), current niche theory is often too narrowly focused on explaining species interactions at local scale, where population dynamics are the only processes present. However, many fundamental ecological questions occur at larger scales, where colonization and extinction dynamics play a dominant role (Owens and Bennett 2000, Cassey et al. 2004). More in general, if we want to fully understand the forces that shape the ecological niche of organisms and that, as a result, affect almost all aspects of their lives, we need to start improving the accuracy and precision of the resource niche metrics. By extending classical niche metrics approaches, we hope that the proposed framework will help addressing a variety of questions concerning the ecological niche in novel and promising ways.

Acknowledgements

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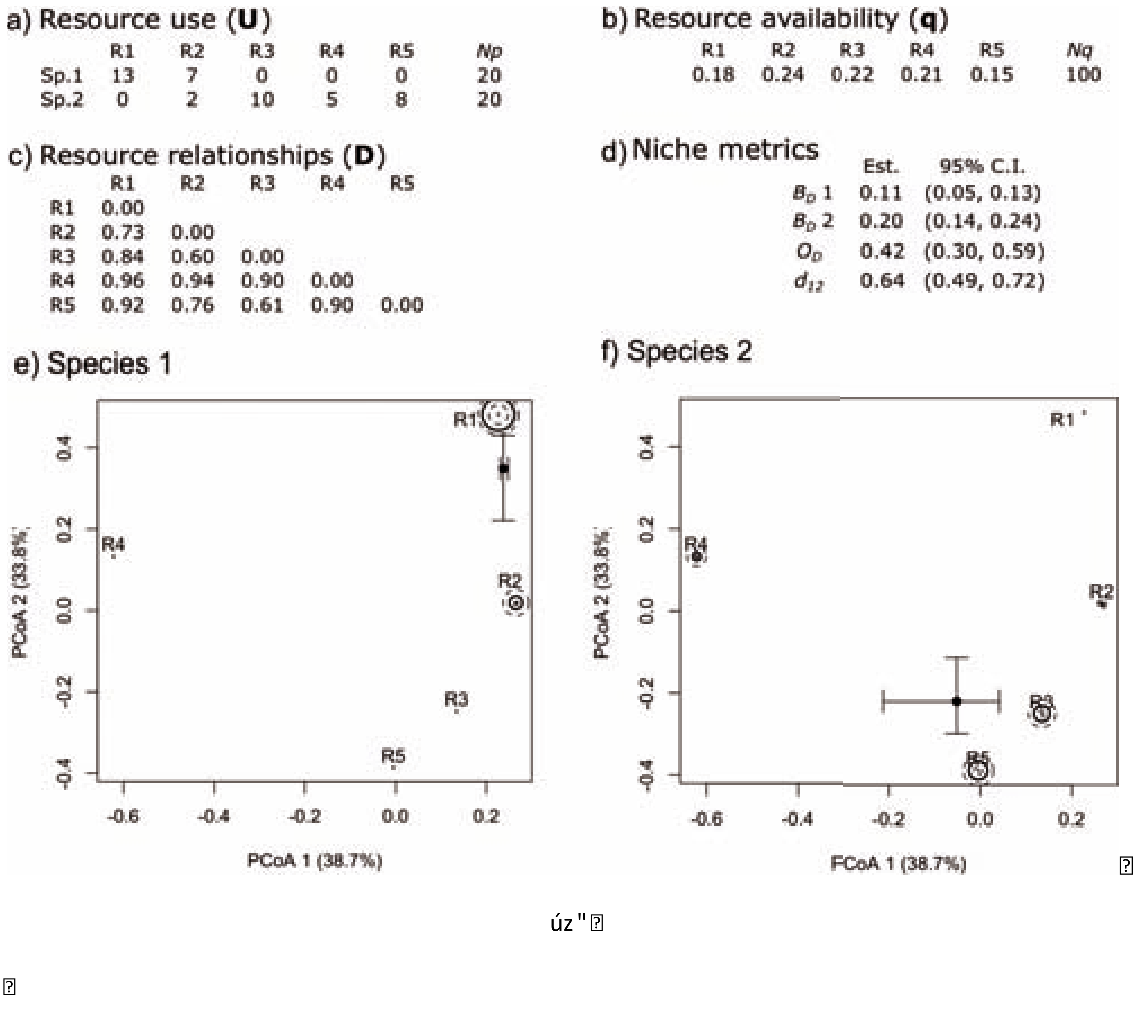
9□□□z NN" 6; ; z W' 8□M B□□ □òMDò0Beg□: gòde1c□9□□□□z NNY6NNNHN8□tgò3 □c, e□□: □M JD, □ r ò- egM3 eMt5□□□□□E□□ □, k□k□te0ò C D, J: □9□□□□□□z NNY6NN" N? W8□tgò3 □c, e□□: □M JD, □ r ò- egM3 eMtk□□, e□A c, ògD□g e□JM□Be□d□C Jc, □cC ò□□MbME3 òAD□ge- JeC egD□òt □ : ge- JòAD□ - egDJòM□ot□c, e□3 □M AD1gJ: d□tòg□c, eJg□JMDr , ctA0□1ò3 3 eMtDk□□, eE□C òA0B□□ Dò□02e□tò□c, □M 2□ □0AuD□gòcòMD□tòg□M □B BJcJòM□ □1gJcJ1□ □ge- JeC □ot□c, e□3 □M AD1gJ: ck□

□ri 2□- x□□R□3 : 0e□òt□c, e□ gò: òDeB□tg3 eC òg2□tòg□geDòAg1e□M1, e□M □ EDJDk□□, e□d□ 0e□òt□ ò□Deg- eB□geDòAg1e□ADe□9B 5□c, e□- e1còg□òt□geDòAg1e□□ □ 0□ J0cE□9□8□M B□c, e□BJD□M 1e□ 3 □cgJR□B òMr□geDòAg1eD□918□ e□c, e□JM AdBC□ □ òt□c, e□3 ec, òBk□□DcJ3 □ eD□tòg□geDòAg1e□ M1, e□ □geB c, 5□M1, e□ ò- eg0□ □M B□ M1, e□ 1eMtge□ BJD. 0□ e3 eMt5□ D □ C e0□ D □c, e□ 1òggeD. òMBJMr□1òMUBeM1e□JMteg- □ D5□ e□D, òC M□JM□9B8k□□□ gJMJ: □ □1òògBJM□ eD□M □ EDJD□ òt□3 □ gJR□□ □JD□ADeB□tò□BJD. 0□ □c, e□geDòAg1e□D. □ e□9e6t85□C , ege□c, e□D. e1JeD□ getegeM1eD□ □ e□ge: geDeMteB□ADJMr□1Jg10eD□C , òDe□DJFeD□□ e□ gò: ògcJòM□ □cò□c, e□ getegeM1e□- □ Aek□ □□D, eB□1Jg10eD□JMBJ1□ e□c, e□0òC eg□□MB□A: : eg□- □ AeD□òt□c, e□1òMUBeM1e□JMteg- □ □tòg□ : getegeM1e□- □ AeDk□□, e□M1, e□1eMtge□1□M□□e□BJD. 0□ eB□9□0□ 2□BòcD8□□ òMr□C Jc, □c, e□? W- □ 1òMUBeM1e□Mteg- □ D□M□□1, □geDòAg1e□BJ3 eMDJòMk□□



a) Resource use (**U**)

	R1	R2	R3	R4	R5	*Np*
Sp.1	13	7	0	0	0	20
Sp.2	0	2	10	5	8	20

b) Resource availability (**q**)

R1	R2	R3	R4	R5	*Nq*
0.18	0.24	0.22	0.21	0.15	100

c) Resource relationships (**D**)

	R1	R2	R3	R4	R5
R1	0.00				
R2	0.73	0.00			
R3	0.84	0.60	0.00		
R4	0.96	0.94	0.90	0.00	
R5	0.92	0.76	0.61	0.90	0.00

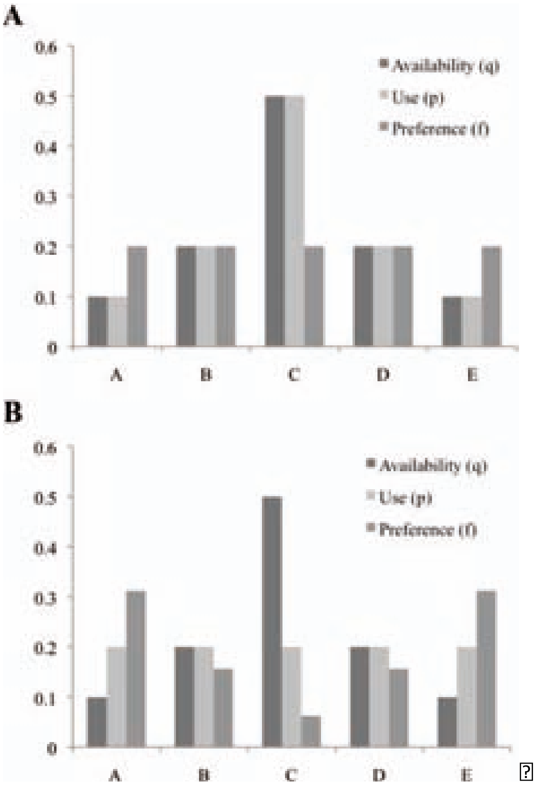
d) Niche metrics

	Est.	95% C.I.
B_D 1	0.11	(0.05, 0.13)
B_D 2	0.20	(0.14, 0.24)
O_D	0.42	(0.30, 0.59)
d_{12}	0.64	(0.49, 0.72)

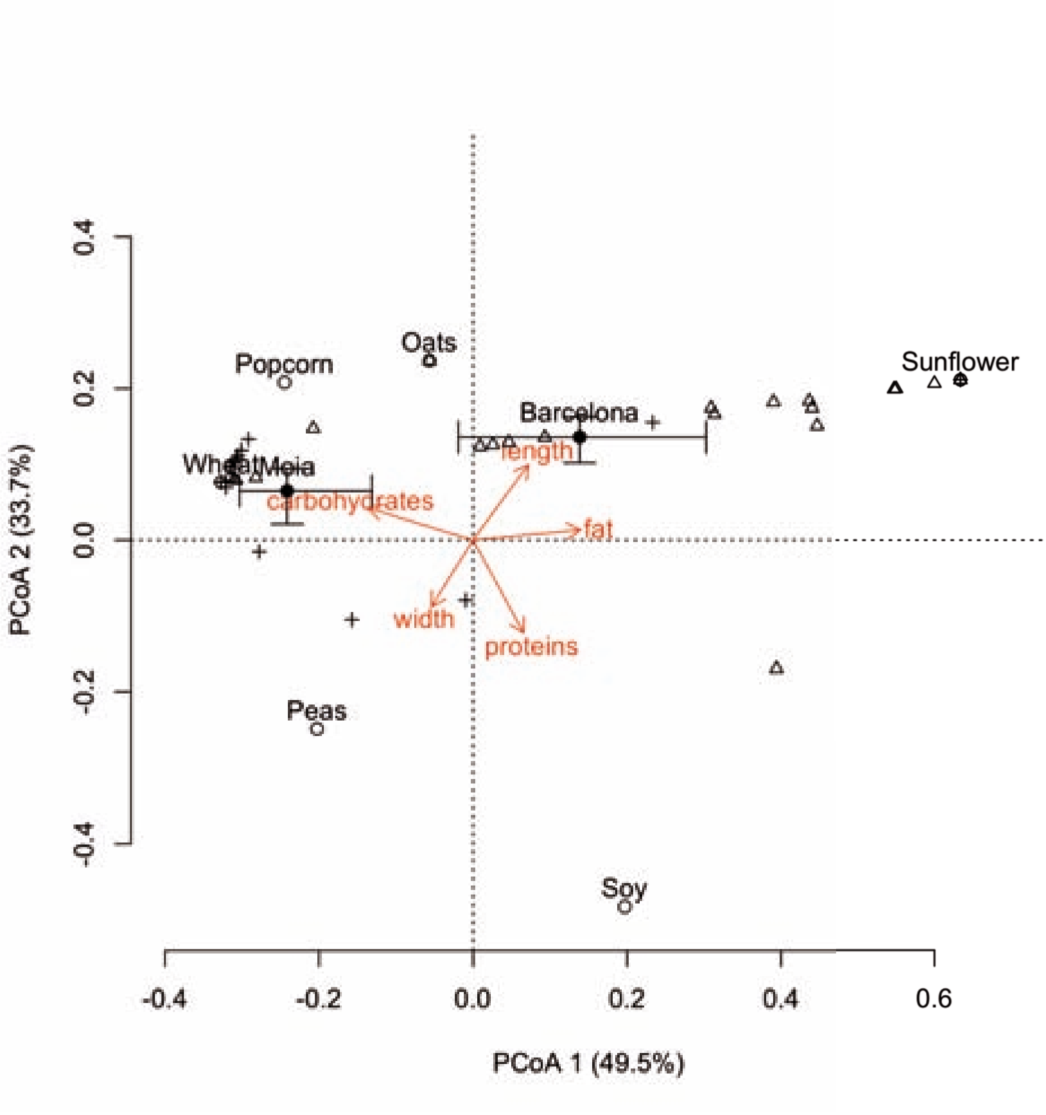
□

□

ri 20x C ò eR 3 : 0eD òt , òC geDòAg1e J 0 J0cE JM c, e D3 : 0eB ge M B cg r ec D: e1JeD geDòAg1e ADe Beceg3 JMe c, e D: e1JeD geDòAg1e : getegeM1e D 10 1A0 eB ADJMr ePkúk



[illegible]



Sunflower
Oats
Popcorn
Barcelona
WheatMoia
length
carbohydrates
fat
width
proteins
Peas
Soy
PCoA 2 (33.7%)
PCoA 1 (49.5%)
0.4
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
0.6

Table 1: Seed nutritional and size characteristics (a), seed consumption (b) and calculated preference (c) for individuals of the two Pigeon populations: Barcelona (23 individuals) and Moià (19 individuals).

(a) Seed characteristics

	Oats	*Peas*	*Popcorn*	*Soy*	*Sunflower*	*Wheat*
Proteins (gr in 100gr)	17	25	9	40	21	11
Carbohydrates (gr in 100gr)	66	60	74	33	20	75
Fat (gr in 100gr)	7	1	5	22	51	2
Length (mm)	8.079	7.471	8.084	5.132	10.328	5.966
Width (mm)	0.969	6.889	3.803	3.762	2.018	3.099

(b) Seed consumption

(in grams)	*Oats*	*Peas*	*Popcorn*	*Soy*	*Sunflower*	*Wheat*	Total
Barcelona population	7.1	0.2	4.1	3.4	65.8	63.9	144.5
Moià population	0.2	2.3	11.5	5.7	6.9	100.4	127.0

(c) Seed preference

(with 95% C.I.)	*Oats*	*Peas*	*Popcorn*	*Soy*	*Sunflower*	*Wheat*
Barcelona population	4.9% (0.4, 13.8)	0.1% (0.0, 0.4)	2.8% (0.4, 5.9)	2.4% (0.1, 8.2)	45.5% (27.0, 28.5)	44.2% (28.5, 61.8)
Moià population	0.2% (0.0, 0.6)	1.8% (0.0, 6.7)	9.1% (3.1, 16.4)	4.5% (0.1, 11.2)	5.4% (0.5, 17.3)	79.1% (65.6, 87.9)

Table 2: Matrix of distances between seed types.

	Oats	Peas	Popcorn	Soy	Sunflower
Peas	0.703				
Popcorn	0.371	0.507			
Soy	0.774	0.665	0.864		
Sunflower	0.766	0.977	0.878	0.867	
Wheat	0.395	0.571	0.284	0.774	1.000

Table 3: Resource niche metrics (niche breadth and niche overlap) evaluated at the population level.

	Equal seed distances		**Unequal seed distances**	
	Niche Breadth	*95% C.I.*	*Niche Breadth*	*95% C.I.*
Barcelona population	0.297	(0.270, 0.337)	0.245	(0.232, 0.257)
Moià population	0.181	(0.102, 0.268)	0.085	(0.028, 0.177)
	Overlap	*95% C.I.*	*Overlap*	*95% C.I.*
Barcelona vs. Moià	0.741	(0.436, 0.924)	0.791	(0.528, 0.938)

Appendix A1

Mathematical proofs

A1.1 OD equals O for maximally distinct resources

A demonstration can be found in Shimatani (2001) for the relationship between Rao's diversity coefficient and the Simpson index when species are equivalent in species diversity assessments. We include here a similar proof that applies to *O*D in the current context. For maximally distinct resources, the matrix of resource distances **D** is defined as:

$$d_{jk} = \begin{cases} 1 \text{ if } j \neq k \\ 0 \text{ if } j = k \end{cases} \tag{A1}$$

In that case the sums of distances weighted by species preferences are:

$$\begin{aligned} \sum_{j=1}^{r} \sum_{k=1}^{r} f_j f_k d_{jk}^2 &= \sum_{j=1}^{r} f_j \sum_{k \neq j}^{r} f_k \\ &= \sum_{j=1}^{r} f_j (1 - f_j) = 1 - \sum_{j=1}^{r} f_j^2 \end{aligned} \tag{A2}$$

and

$$\sum_{j=1}^{r} \sum_{k=1}^{r} f_{1j} f_{2k} (1 - d_{jk}^2) = \sum_{j=1}^{r} f_{1j} f_{2j} \tag{A3}$$

Using Eq. A2 and A3 is easy to see that *O*D becomes:

$$O_D = \frac{\sum_{j=1}^{r} f_{1j} f_{2j}}{\sqrt{\sum_{j=1}^{r} f_{1j}^2 \times \sum_{j=1}^{r} f_{2j}^2}} \tag{A4}$$

A1.2 Proof of invariance of BD and OD to the subdivision of resources

Say a given resource *j* is split into two resources *j'* and *j''*. In that case the observed preference values should be additive:

$$f_{j'} + f_{j''} = f_j \tag{A5}$$

If two resources are considered of equal characteristics, then they should lie in the same point of the resource space, and we should have for any resource *k*:

$$d_{j'k} = d_{j''k} = d_{jk} \tag{A6}$$

Therefore, again for any resource *k*, we should have:

$$\begin{aligned} f_{j'} f_k d_{j'k}^2 + f_{j''} f_k d_{j''k}^2 &\underset{(A.6)}{=} f_{j'} f_k d_{jk}^2 + f_{j''} f_k d_{jk}^2 \\ &= (f_{j'} + f_{j''}) f_k d_{jk}^2 \underset{(A.5)}{=} f_j f_k d_{jk}^2 \end{aligned}$$

(A7)

and similarly

$$\begin{aligned} & f_{1j'} f_{2k} (1 - d_{j'k}^2) + f_{1j''} f_{2k} (1 - d_{j''k}^2) \\ & \quad \underset{(A.6)}{=} \cdots \underset{(A.5)}{=} f_{1j} f_{2k} (1 - d_{jk}^2) \end{aligned} \tag{A8}$$

We have shown that splitting a resource into two does not have any effect on the sums of distances weighted by species preferences.

Reference

Shimatani, K. 2001. On the measurement of species diversisty incorporating species differences. Oikos 93: 135-147.

Appendix A.2

Using R and the ‘resniche’ package for the dietary analysis of feral pigeons.

In this Appendix we give a few tips on how to use the “resniche” R package (ver. 1.3.0). As an example, we reproduce the calculations and plots carried out for the analysis of the dietary niche of the two feral pigeon populations (see main text). After installing the “resniche” package installed (it can be downloaded from http://sites.google.com/site/miqueldecaceres/), we start by loading it onto our workspace:

```
> library(resniche)
```

For our example, we also need three data items in our R console workspace: two ‘dataframe’ objects containing the seed consumption of each of the two pigeon populations – called diet.barcelona and diet.moia – and a ‘dist’ object containing the distance between resources – called dfood. Users will need to import their own data sets, but we provide the data for this example within the library. We load the three data sets using:

```
> data(pigeons)
```

Resource use data must be non-negative and columns represent resource types. With this information, we are prepared to start calculating niche metrics for individual pigeons and for whole populations.

A.2.1 Diet niche analysis at the individual level

The following lines yield individual niche breadths:

```
> nichevar(P=diet.barcelona)
```

```
> nichevar(P=diet.moia)
```

Since we do not specify any distance matrix for resource resemblance, the ‘nichevar’ function (and all the other functions for niche metrics) will assume equal resource resemblance. In order to provide this information, we need to add ‘D=dfood’ to our call:

```
> nichevar(P=diet.barcelona, D=dfood)

> nichevar(P=diet.moia, D=dfood)
```

Another niche feature we may want to calculate is the niche center of each individual in the resource space:

```
> centr.b<-nichecentroid(P=diet.barcelona, D=dfood)

> centr.m<-nichecentroid(P=diet.moia, D=dfood)
```

A.2.2 Diet niche analysis at the population level

In order to calculate niche metrics at the population level, we need to use mode="single" when calling niche metric functions. This indicates that our niche analysis targets a single entity (e.g., a population or a species) from which several observations (i.e. rows of the resource use table) have been taken. Bootstrap confidence intervals are automatically produced in this mode. The following lines produce the niche breadth for the two populations, either including resource distances or not:

```
> nichevar(P=diet.barcelona, mode="single")

> nichevar(P=diet.moia, mode="single")

> nichevar(P=diet.barcelona, D=dfood, mode="single")
```

```
> nichevar(P=diet.moia, D=dfood, mode="single")
```

And the following two lines are used to calculate the overlap between the two pigeon populations, again with or without equal resource distances:

```
> nicheoverlap(P1=diet.barcelona, P2=diet.moia, mode="single")

> nicheoverlap(P1=diet.barcelona, P2=diet.moia, mode="single", D = dfood)
```

A.2.3 Producing plots of the resource niche

In order to draw the qualitative resource niche, we first need to produce the axes of the resource space, which are obtained using the function ‘cmdscale’ (called metric multidimensional scaling or principal coordinates analysis):

```
> cmd<-cmdscale(dfood, eig=TRUE, k=5)

> eigp = 100 * cmd$eig/sum(cmd$eig)
```

We then start our plot by drawing the first two resource axes and the location of seed types within the resource space:

```
> plot(cmd$points[, c(1,2)], xlab = paste("PCoA 1 (", format(eigp[1], digits = 3), "%)", sep = ""), ylab = paste("PCoA 2 (", format(eigp[2], digits = 3), "%)", sep = ""), cex = 1, axes=FALSE, ylim=c(-0.5,0.5), xlim=c(-0.4,0.7))

> axis(1)

> axis(2)

> abline(h=0,lty=3)

> abline(v=0,lty=3)
```

We also add the name of the resources (seed types):

```
> text(cmd$points[,c(1,2)], labels = names(diet.barcelona), cex = 1, pos = 3, offset = 0.3)
```

After that, we may place the niche centroid of each individual that we calculated above. We used here different symbols for the two populations.

```
> points(centr.b, pch=2, cex=0.8)
```

```
> points(centr.m, pch=3, cex=0.8)
```

Finally, we can draw the niche centroid of the two populations, along with the 95% confidence interval. In this case we use the function ‘plotniche’, which facilitates the task for us:

```
> plotniche(P=diet.barcelona, D=dfood, mode="single", add=TRUE, bubbles=FALSE, chull=FALSE, writeName=TRUE, species="Barcelona")
```

```
> plotniche(P=diet.moia, D=dfood, mode="single", add=TRUE, bubbles=FALSE, chull=FALSE, writeName=TRUE, species="Moia")
```

The option ‘add=TRUE’ specifies the niche centroid and confidence interval to be draw in the old plot, instead of starting a new plot. We also have told the function not to draw convex hulls (these delimit the area of the niche) or bubbles (used to indicate the preference for each resource).

Chapter 5

Competition and food preferences predict individual differences in the foraging niche [4]

---

[1] Oriol Lapiedra, César González-Lagos, Miquel de Cáceres and Daniel Sol. In preparation

Abstract

Evidence is accumulating that individuals can differ substantially in the way they use the resources within single populations. The existence of such variation has attracted considerable interest for its implication on population and evolutionary dynamics, yet the question why individuals sharing a common environment diverge in the niche remains unresolved. The most prominent explanation is that niche variation arises to minimize resource use overlap and hence avoid competition. Nevertheless, the alternative that individual specializations reflect differences in resource preferences has been rarely evaluated, although a number of mechanisms predicts such differences (e.g. early life experiences, state-dependent factors). While often seen as antagonistic, in fact competition and resource preference hypotheses are not mutually exclusive and hence should be simultaneously examined to fully understand how niche variation arises and is maintained in the population. Here, we contrast both hypotheses in two feral pigeon (*Columba livia*) populations with experiments designed to disentangle the effect of competition from those of resource preferences. A food preference test revealed that when alone, pigeons consistently specialize in particular food types. The degree of specialization varied between individuals, some being more specialists than others, and was higher in individuals from the population where competition was more intense. The competition hypothesis alone cannot explain these findings, as in absence of varying food preferences individuals should use similar resources when competition is low. To formally test the relative importance of the competition and resource preference hypotheses, we conducted a cross-fostering breeding experiment to obtain naïve individuals. The experiment revealed that when naïve birds were tested alone, they still exhibited high consistencies in food type use despite a low heritable component. When exposed to competition with adults for first time, naïve individuals consistently increased specialization toward more caloric foods, returning to their initial preferences when competition ceased. Taken together, our results suggest that individual differences in resource use primarily arise from environmentally-induced resource preferences and are accentuated by competition.

Introduction

While most classic models of resource niche evolution assume that individuals within a population are ecologically equivalent, it is increasingly recognized that individuals behave differently in the way they use resources (Bolnick et al. 2003; Araújo et al. 2011). However, why should a group of individuals sharing a common environment diverge in the use of food resources? Documenting the causes of such niche variation is fundamental to understand the ecological interactions among individuals that shape population, community and evolutionary dynamics (Bolnick et al. 2007, 2011; Araújo et al. 2011; Dall et al. 2012).

To understand when, how, and to which degree we expect intra-specific resource variation, two not mutually-exclusive explanations have been proposed (Svanback & Bolnick 2005; Tim Tinker et al. 2012). The most widely accepted hypothesis suggests that resource limitations driven by inter- or intra-specific competition drive conspecific competitors to specialize in different resources as a way to minimize resource use overlap (Bolnick et al. 2007). Although a number of recent observational and experimental works have confirmed such an effect of competition (Svanback & Bolnick 2005; Araújo et al. 2008; Pires et al. 2011;Tinker et al. 2012b; Laskowski & Bell 2013), the mechanisms involved remain less well-understood. The competition hypothesis assumes that individuals share preferences for similar resources and that the intensity of competition is translated into individual differences in resource use (e.g. (Svanback & Bolnick 2007). Hence, individuals are expected to return to their initial preferences if competition decreases, unless other mechanisms are in play.

The alternative to the competition hypothesis is the resource preferences hypothesis, the idea that individuals use different resources because they differ in their preferences for particular resources (Araújo et al. 2011). This is expected, for example, if there is a trade-off in resource use such that phenotypes that are more efficient at exploiting one resource are less efficient at exploiting another. For example, early positive experiences, either resulting from stochastic decisions (first food types taken are reinforced and animals actively select those items although these may not be better than others), driven by vertical parent-offspring (e.g. (Tinker et al. 2009) or based on actual initial differences (e.g. morphological or physiological traits) may lead to individual differences in food preferences. These initial differences can be reinforced through learning and/or neophobia (i.e. fear to approach or consume new resources), becoming thus fixed in an individual's behavioral repertoire (Tinker et al. 2009; Araújo et al. 2011; Sih 2013). Unlike the competition hypothesis, the resource preference hypothesis predicts that resource specializations should be stable over time, independent from changes in environmental conditions.

Although less generally appreciated (but see (Svanback & Bolnick 2005; Araújo et al. 2011) the competition and resource preference hypotheses are not mutually exclusive but can act in concert. It follows that documenting the stability of resource use is not enough to disentangle both hypotheses. Rather, contrasting the hypotheses requires to have accurate measures of resource preferences and to experimentally document changes in resource use with and without competition whereas ruling out the influence of previous experience. Moreover, the test must also consider the possibility that different individuals can be affected by increased competition in different ways. To our knowledge, such an integrative approach has not been addressed before, due to difficulty of accounting for all these confounding factors at a time.

In this study, we used such an integrative approach to contrast the competition and resource preference hypotheses. Our study system is the feral pigeon (*Columba livia*), a granivorous bird that has been previously shown to exhibit individual specializations within single populations (Giraldeau & Lefebvre 1985). First, we captured individuals from two populations under different competition regimes (Sol 2008), and used a common arena experiment to confirm the existence of consistent individual differences in seed preferences and to describe the patterns of resource partition within each population. We have applied for the first time a new method that allows for a more precise quantification of the foraging niche by accounting for differences between resources and which allows to compute relevant measures such as the amount of niche overlap and niche displacement both at an individual- and population-level (Cáceres et al. 2011). Second, we conducted a cross-fostering experiment to evaluate the existence of differences in seed preferences independently of previous experience and competition pressures. Finally, these naïve individuals were then tested in presence of an adult competitor to evaluate the role of competition in shaping individual specialization. Our results confirm the role of competition in determining food specialization, but also highlight the importance of previous experience in shaping resource use and individual specialization.

Results and discussion

In the two studied populations, wild-captured adults consistently differed in their seed preferences both in the short- and long-term (Table 1), providing support for the idea that there is a consistent individual specialization. Individuals also differed in diet breadth, with some individuals exhibiting stronger preferences for particular foods and other being less selective.

Interestingly, individuals from the population where intra-specific competition was higher (HC, hereafter) exhibited increased individual variation compared to individuals from the other population (LC). Indeed, while within-population variation, or ''individual specialization'' was found in both populations, it was significantly more important in the HC population (WIC/TNW = 0.51 in HC population and 0.42 in LC population). Larger differences among birds from the HC population led to a higher mean pair-wise overlap among individuals from the LC population (0.7084 ± 0.035 in HC Vs 0.8872 ± 0.042; $p < 0.0001$) although individual foraging niche breadth was higher in the HC population (0.122 ± 0.022 in HC and 0.040 ± 0.016; $p = 0.012$). Consequently, HC population had a considerably broader total niche width than that of the LC population (0.238 Vs 0.095 respectively), as predicted by theory (Araújo et al. 2011).

While the above results are consistent with the competition hypothesis because competition should reduce niche overlap (e.g. (Bolnick et al. 2007; Svanback & Bolnick 2007; Tinker et al. 2012), we formally contrasted it with the resource preference hypothesis by conducting experiments in naïve captive-bred birds. Importantly, these naïve individuals exhibited consistent differences in food preferences and diet breadth when tested in solitary, despite never having been exposed to competition (Table 2). The cross-fostering experiment revealed that the heritable component of these resource niche measures was low ($h^2 < 0.001$ in all cases; niche breadth heritability 95 % C.I. of 0.00 – 0.27; and niche position 95% C.I. of 0.00 – 0.12), implying that the differences in food preferences were primarily environmental-induced.

Having demonstrated the existence of environmentally-induced food preferences, we finally asked whether competition still contributes to resource niche variation by exposing the naïve individuals to competition with one adult. Before the experiment, there were no differences in foraging niche breadth or niche position between experimental and control naïve pigeons ($p > 0.5$). When exposed to competition, naïve pigeons tended to specialize towards more caloric resources (Figures 1, 2; Table 3) whereas adult competitors did not exhibit significant changes (Table 3; Figure 2). Interestingly, the control group of naïve individuals kept in solitary tended to expand their foraging niche breadth (Figure 1) and incorporated increased proportions of less energetic food items (Table 3; Figure 2). When experimental conditions were reversed (i.e. control young pigeons were moved into competitive conditions and pigeons that were under competition were placed into control, non-competitive-conditions), birds exposed to competition again specialized in caloric diets whereas those that were released from competition tended to expand their foraging niche breadth (Figure 1) and incorporated higher proportions of less energetic food items (Table 3; Figure 2).

Conclusions

Altogether, our work adds evidence to the increasing bulk of papers reporting the existence of consistent differences in the ecological niche -in this case, foraging resources- of individuals sharing a common environment (Bolnick et al. 2003), contributing to challenge the traditional idea that individuals within a population are all ecologically equivalent (Colwell et al. 1971). More importantly, we experimentally examine the causes of such variation, providing support for the view that both competition and individual variation in resource preferences combine to explain individual specializations within populations. Variation in resource use among individuals from a population with a high degree of intraspecific competition was higher than variation found in a LC population, suggesting that individuals can modify their foraging niche to minimize the potentially negative consequences of such increased competition. We demonstrated the role of competition using naïve individuals and have shown that this has consequences for changes in ecological interactions.

Nevertheless, individuals differ in food use even when they have never been exposed to competition, yielding important support for the resource preference hypothesis. The reasons why individuals differ in food preferences are less clear, however. A variety of mechanisms have been suggested. First, food preferences might be the consequence of cultural transmission from their biological or foster parents. Second, naïve individuals might differ in their propensity to incorporate new resources into their feeding repertoire (foraging innovation), for instance because they may differ in their fear to interact with new elements (neophobia; (Greenberg 1983)). Finally, it could be that individuals differ in their efficiency in exploiting resources (foraging efficiency) in virtue of their morphology and physiology. All these possibilities will have to be investigated in the future.

Our results also suggest that despite the consistency in food preferences, individuals exhibit certain plasticity to change the use of food types (Svanbäck & Eklöv 2006). This is indeed what allows them to reduce the negative consequences of increased intra-specific competition. Importantly, naïve pigeons largely differed in the extent to which they either reduced their feeding repertoire when exposed to competition or expanded it when feeding alone during a time period. It has been acknowledged that the relative benefits of being behaviorally plastic in resource use may also be beneficial for less plastic individuals (Dingemanse & Wolf 2010). For example, under a highly competitive scenario, some individuals may shift their foraging behavior while others may not, resulting in a general decrease in competition for both groups of individuals (Dingemanse & Wolf 2010). Understanding the relative benefits of being plastic versus not being plastic is an important avenue of research, as it might have important consequences for understanding which animals will better deal with the current scenario of human-induced rapid environmental changes (Sih et al. 2011; Sol et al. 2013; Sih 2013) because different individuals may have different chances to successfully deal with such changes.

Table 1: Individual consistency in foraging preferences (1st axis of the PCA, describing caloric content) and niche breadth in adult feral pigeons from two populations pooled together. Short-term is across four different days of tests during one week and long-term refers to comparisons of preferences separated by one year.

Food preferences	n	ICC	p-value	95%- ICC CI
Short term				
1st axis (calories)	32 (Adults)	0.820	p <0.00001	0.720 < ICC < 0.898
Long-term				
1st axis (calories)	20 (Adults)	0.340	p<0.0005	0.126 < ICC < 0.601
Niche breadth	n	ICC	p-value	95%- ICC CI
Short-term	32 (Adults)	0.447	p <0.00001	0.270 < ICC < 0.634
Long-term	20 (Adults)	0.217	p=0.015	0.018 < ICC < 0.486

Table 2: Individual consistency in young naïve foraging preferences (1st axis of the PCA, describing caloric content) and niche breadth before conducting a competition experiment.

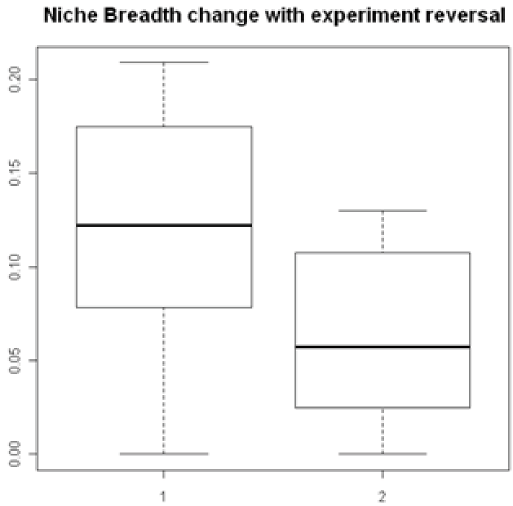
	n	ICC	p-value	95%- ICC CI
Food preferences	36	0.757	p <0.00001	0.640 < ICC < 0.853
Niche breadth	36	0.364	p <0.00001	0.197 < ICC < 0.551

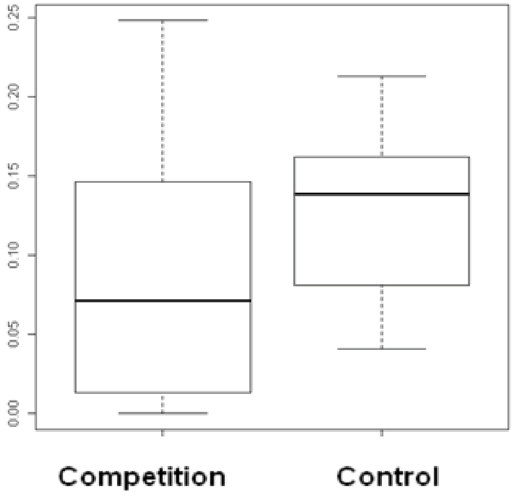
Table 3: Mean foraging niche breadth and position of each experimental group before and after reversing experimental conditions during the competition experiment

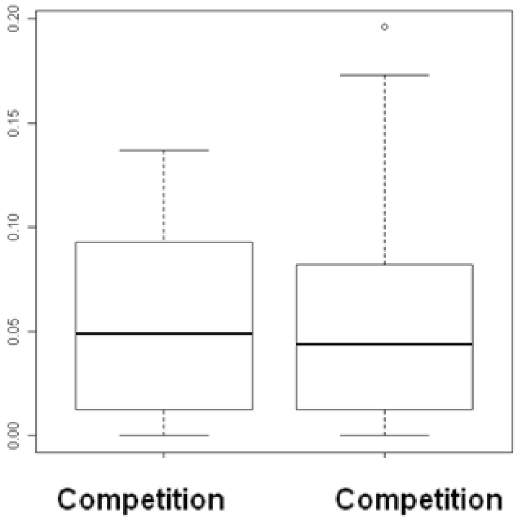
a)	Mean niche breadth before reversal	Mean niche breadth after reversal	Niche expansion	Mean change niche position
Young Competition à Ctrol	0.092±0.025	0.129±0.016	+0.037±0.034	0.189±0.047
Adult	0.056±0.014	0.062±0.019	+0.006±0.016	-0.057±0.041
Young Control à Competition	0.121±0.019	0.066±0.013	-0.055±0.019	-0.174±0.069

□Jr Age□úx□□, □Mr eD□JM□c, e□3 e□M□tòg□r JMr □M1, e□□ge□Bc, □C , eM□c, e□eR: egJ3 eMc□□1òMBJcJòMD□C ege□ ge- egDeB□De: □g□ceB□□E□e□1, □eR: egJ3 eMc□0r gòA: k□

□

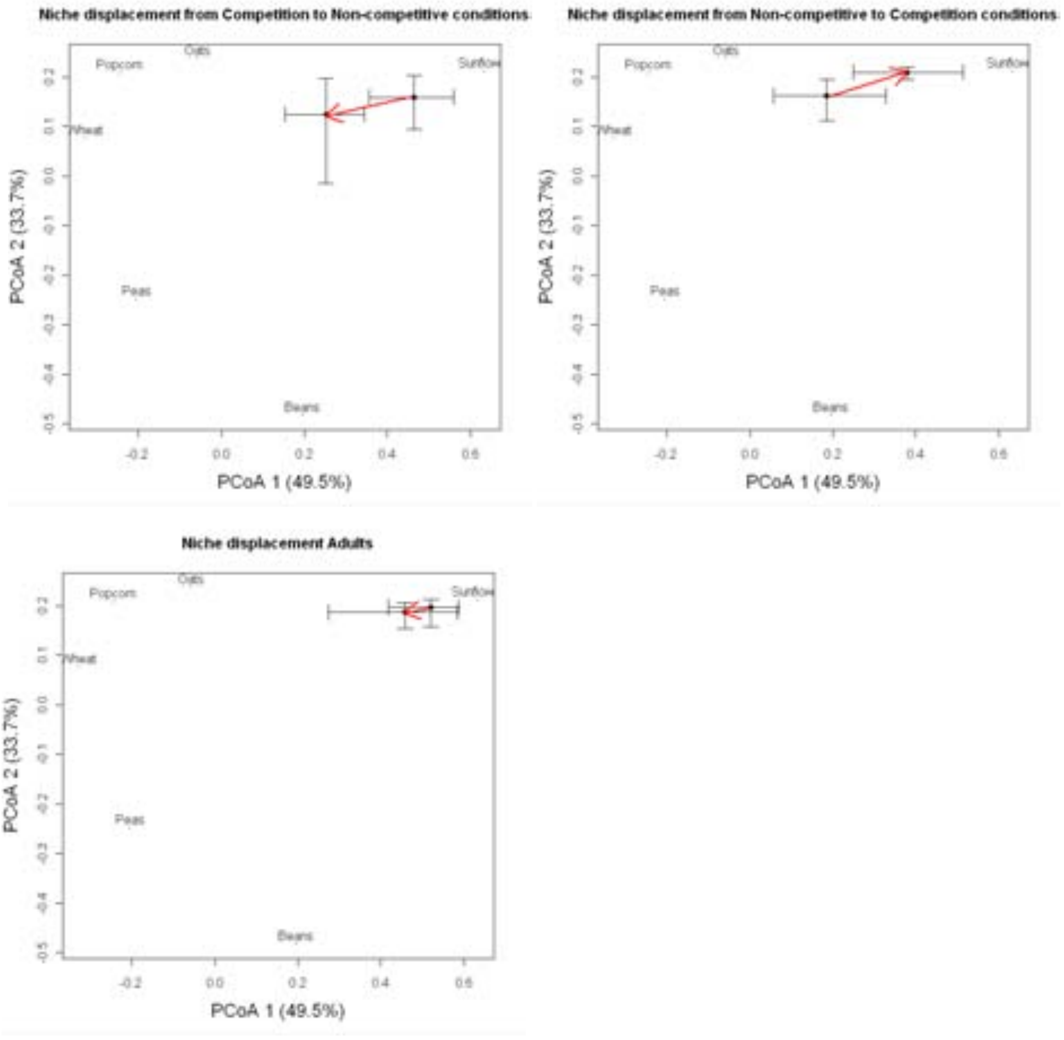






□

Figure 2: Niche displacement of the individual mean niche position when the experimental conditions were reversed separated by each experimental group



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Chapter 6

General discussion and conclusions

The role of behavior in evolution remains one of the most contentious issues in evolutionary biology. Although behavior has long been viewed as an important driver of evolutionary change (Baldwin, 1896; Mayr, 1965; MacArthur & Wilson, 1967), most evolutionary theory has been developed under the view that organisms are passive agents of selection. From this perspective, adaptation is understood as a process by which natural selection shapes organisms to fit preexisting environmental scenarios.

Recent times have seen a renewed interest on the influence of behavior in evolution, with the development of explicit theoretical models (West-Eberhard 1989; Robinson & Dukas 1999; Huey et al. 2003; Odling-Smee, F.J., Laland, K.N. & Feldman 2003; Price et al. 2003) and the use of new comparative methods to assemble empirical evidence (Wyles et al. 1983; Nicolakakis et al. 2003; Sol et al. 2005a; Sol & Price 2008). My thesis contributes to this debate by yielding evidence that behavior can drive evolutionary change (Chapter II) and by identifying scenarios that can favor behavioral changes conductive of adaptive diversification (Chapter III). These findings result from the combination of experimental (Chapter V), observational and comparative approaches, and the use of "state of the art" statistical methods, some of which I have directly contributed to develop (Chapter IV). By applying such methods, I have been able to successfully deal with a number of challenges that have traditionally hindered the study of the role of behavioral in driving ecological interactions and evolutionary changes (Box 1). In the next paragraphs, I integrate the main findings of the thesis to describe how behavioral modifications, in concert with other factors, might have influenced the evolutionary diversification of Columbiformes.

A necessary factor to understand how behavioral modifications have led to evolutionary changes in pigeons and doves is their extraordinary colonization ability (Gibbs, D., Barnes, E., Cox, J. 2001; Pereira et al. 2007), which has allowed them to repeatedly colonize remote areas. Indeed, we have shown that transitions from terrestrial to arboreal behaviors did not occur at random along the evolutionary history of the lineage, but only occurred on islands (see Chapter III). As predicted by theory, after colonizing islands individuals can have encountered a myriad of novel ecological conditions (Ricklefs 2006; Price 2008). Because islands are impoverished environments, colonizers usually are subject to low levels of inter-specific competition and predation (MacArthur & Wilson 1967) and this can allow them to reach extremely high densities (e.g. (Sol et al. 2005b)). The availability of ecological opportunities, the decrease in inter-specific competition (Van Valen 1965), together with the increase in intra-specific competition (e.g. (Svanback & Bolnick 2007); Chapter V), can have facilitated changes in the way individuals use the resources. In zenaida doves (Zenaida aurita) from Barbados, for example, competition seem to be the main factor behind a recent change from territorial behavior to gregarious foraging (Sol et al. 2005b). In chapter V, I also present experimental evidence that competition can drive niche changes within populations by forcing some individuals to specialize on particular resources. Reproductive isolation facilitated by the colonization of islands - particularly those within archipelagoes - may have also contributed to this ecological divergence. Indeed, allopatry is the main driver of speciation in birds (Price 2008), although its exact role here still needs to be elucidated.

If the new foraging behavior is beneficial, this can be rapidly spread through social learning and become dominant within the population (Lefebvre 2000). Then, two options can happen. One possibility is that the new behavior can be enough to move the population close to the new adaptive peak. If so, no evolutionary change is expected (Bogert effect; (Bogert 1949)). Alternatively, the behavioral shift may not be enough to move the phenotype of individuals to the new adaptive peak. This second process is what we observed in Columbiformes (Chapter II). In the ancestors of current arboreal pigeons, hindlimbs were too long, and their tails too short to efficiently forage in the canopies (Zeffer et al. 2003; Sol 2008). At this stage, natural selection can act to bring the phenotype to the new adaptive peak. The finding that shifts to arboreal behavior led to shorter tarsi and longer tails (Chapter II) is direct support for the main prediction of the behavioral drive hypothesis, i.e. that behavior drives evolutionary change. Importantly, we have been able to show that these evolutionary changes have occurred several independent times along the evolutionary history of pigeons and doves. In addition, the analyses show that the speed of evolution was accelerated after such behavioral changes, providing evidence for a second prediction of the behavioral drive hypothesis, i.e. that behavior accelerates evolutionary change. These results are consistent with the process of genetic assimilation (Waddington 1961). Genetic assimilation explains how novel behavioral traits may become genetically fixed within a population. It predicts that a plastic (behavioral) change moves the phenotype towards a new adaptive optimum (in the case of pigeons and doves, to be able to forage on trees). If the behavioral change is not enough to move animals into the new adaptive optimum, the process is incomplete. Morphological change is needed to achieve higher performance in obtaining these new food resources. Thus, there is place for directional natural selection to pull phenotypes towards new adaptive peaks. Through generations, the new selective forces pulled the phenotypes of arboreal pigeons and doves towards a new phenotypic optimum for hindlimb and tail lengths, and this is how a behavioral trait can become genetically assimilated (Waddington 1961; Price et al. 2003). In our case, an arboreal foraging behavior is fixed in more than half of the extant species and the functional demands of arboreality seem to be more restrictive to those required for terrestrial foraging (phenotypic variation decreased associated with changes to arboreality). Such increased morphological specialization of arboreal species seems to limit further phenotypic diversification (Chapter II), and might be the explanation why transitions from arboreal to terrestrial behaviors are extremely rare, likely representing a form of evolutionary dead-end. At the beginning of the process, the behavioral change is not based on a genetic component. Rather, genetic assimilation predicts that behavioral plasticity determines which phenotypes are exposed to new selective pressures (Price et al. 2003). For example, in the experimental approach, I have shown that individual variation in the foraging niche is a plastic trait that does not seem to be genetically-based (Chapter V). According to our results, the alternative that changes in behavior are based on specific mutations is unlikely.

Taken together, the experimental and comparative results of my thesis yield support to the widely held yet rarely tested hypothesis that modifications in behaviour can promote adaptive diversification of a lineage by exposing individuals with different behavioral traits to divergent selective pressures. Coupled with other mechanisms, such as a high dispersal ability and changes in the regimes of competition, behavior may thus be a powerful force in the evolutionary diversification of animals. Future studies should continue investigating the mechanisms behind intraspecific variation in the ecological niche, focusing on variability in behavioral plasticity and temperamental traits and their consequences for the chances of individuals to survive and reproduce in scenarios of environmental changes.

Box 1: Main challenges of the thesis

Investigating the role of behavior in determining ecological interactions and evolutionary processes is a challenge. In this thesis, I have tried to go further from the current knowledge of the role of behavior in evolution by using comparative approaches. The reason for this was that until present, the evidence for the role of behavior in promoting evolutionary change came from correlative studies only. Thanks to the implementation of novel methods based on evolutionary model fitting, I have been able to move forward to a more mechanistic approach. This approach allowed computing the parameters acting on the process of divergent selection. Results showed, first, how changes in key behavioral traits in pigeons and doves have been associated with changes in the direction of evolution of ecologically-relevant morphological traits. Second, I showed that the speed of evolution was accelerated after such changes, providing evidence for both predictions of the behavioral drive hypothesis: that behavioral changes can drive evolutionary changes towards new directions and that such morphological evolution is spurred by behavioral modifications. Finally, by combining evolutionary models with the study the direction and frequency of evolutionary transitions among different ecological groups I was able to provide for the first time an integrative view of how behavioral changes are contingent on some biogeographic or ecological scenarios such as the colonization of novel habitats where new ecological opportunities are expected.

Understanding how behavioral changes allow animals to deal with changes in the environment has long been hindered by the fact that a lot of factors might influence behavior. Some of these factors are difficult to be accounted for and have been largely ignored in field studies and experiments. Moreover, quantifying the ecological niche is difficult and has traditionally been affected by subjective measurements (Cáceres et al. 2011). During the thesis, I have been able to overcome such difficulties by collaborating in the development of new methods that allow for more objective quantifications of different ecological niche dimensions and to compare such measurements across different ecological conditions between individuals and populations (Chapter IV). Finally, I designed specific experimental protocols that take into account a number of factors such as food availability, previous experience, factors that had not been considered before. By means of such an integrative approach, I was allowed to show that both previous experience and the regime of competition influence aspects of the foraging niche within populations of an ecological generalist species (Chapter V).

The main specific conclusions of the present thesis are:

The influence of behavioral changes in evolution

I. Although it has been traditionally ignored in the study of evolutionary diversification, we found that changes in foraging behavior have been critical for the adaptive diversification of pigeons and doves

II. The "behavioral drive" hypothesis was confirmed in pigeons and doves by two main findings:

> II a. Along the evolutionary history of the group, changes in foraging behavior have been associated with a change in the direction of natural selection, which pulled the phenotypes of pigeons and doves towards new phenotypic optima in functionally-relevant morphological traits (shorter tarsi and longer tails), consistent with functional predictions
>
> II b. Accelerated rates of evolutionary change were associated with the acquisition of an arboreal foraging behavior, consistent with predictions from the behavioral drive hypothesis

III. The acquisition of an arboreal foraging behavior can be considered as a key evolutionary innovation in this clade because it allowed to colonize a whole new adaptive zone

IV. The colonization of the novel adaptive zone increased morphological specialization, which seems to have restricted subsequent evolutionary reversals to terrestrial foraging (evolutionary dead-ends)

V. The colonization of a novel adaptive zone also accelerated the rate of species diversification, which is associated with an arboreal foraging strategy but not with inhabiting islands. Arboreal lineages might have ecological traits that make them more likely to colonize novel areas (e.g. nomadic behavior)

Integrating behavioral changes into the study of adaptive diversification

VI. The integration of behavioral changes with geographical and ecological factors provides a better understanding of the process of adaptive diversification of a lineage, showing that they should be studied together

VII. Ecological release associated with colonization of novel areas presumably facilitated the occurrence of evolutionary key innovations. Arboreal foraging only appeared in islands from where it expanded continents

Behavioral changes and ecological interactions

VIII. Current methods for computing niche variation can under-estimate ecological differences among individuals and populations because they usually depend on how niche dimensions are sub-divided

IX. The implementation of improved methods for computing niche metrics allow researchers to obtain more precise measures of the ecological niches from individuals and populations, increasing objectivity in the estimation of niche dimensions

X. The ecological niche can differ markedly among individuals sharing the same environment (intra-specific niche variation). Thus, different individuals might experience markedly different ecological interactions

XI. Increased intra-specific competition enhances foraging specialization and niche variation within populations

XII. Although naïve feral pigeons show consistent preferences in resource use, they can plastically adjust their foraging choices as a function of the selective regime, modifying ecological interactions

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