SPATIAL PROCESSES IN ECOLOGY AND EVOLUTION, 
AND IMPLICATIONS FOR CONSERVATION

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ACADEMIC DISSERTATION

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HELSINKI 2015
“[...] provability is a weaker notion than truth”

Douglas R. Hofstadter
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The thesis constitutes of the following articles, which are referred to in the text by their Roman numerals:

I  Ramiadantoa T., Sirén J. and Hanski I. Phylogenetic inference of geographical radiation – Submitted manuscript.

II  Ramiadantoa T. and Ovaskainen O. Generalist-specialist coexistence in fragmented landscapes-Submitted manuscript.


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Habitat loss and fragmentation is the main culprit behind the current decline in biodiversity. The estimated current rate of extinction is two or three orders of magnitude higher than the background extinction rate. This thesis analyzes existing data and develops models to improve our understanding of the role of spatial processes in the dynamics of populations and communities. This work is focused on the features of habitat destruction that causes decline of biodiversity as well as the traits that make species vulnerable to habitat loss.

First, I attempt to infer relationships between spatial heterogeneity, rate of diversification (speciation and extinction), and the dynamics of geographical ranges from a reconstructed phylogeny. I build a flexible comparative method to analyze adaptive radiation and range dynamics that extends the current models in two directions by allowing more than two regions and by assuming diversity-dependent diversification rates. In a five-region system stimulated by the biogeography of Madagascar, processes that increase and decrease diversity are strongly correlated. Therefore, it is not possible to estimate independently region-specific speciation and extinction rates, though their ratios can be successfully estimated. When applied to Malagasy dung beetles, we found that diversification rate is highest in the northern (very heterogeneous) and lowest in the southern (most homogeneous) parts of Madagascar. Thus it appears that landscape heterogeneity promotes diversification and thus biodiversity.

The two other chapters investigate the consequences of habitat loss and fragmentation for generalist and specialist species. We aim to understand how generalist and specialist species respond to habitat loss and fragmentation. In particular, we ask why generalist species often increase in abundance following an intermediate level of habitat destruction. I develop a modular modeling approach that allows one to switch on and off various mechanisms as needed. This approach one to assess the marginal and joint effects of different mechanisms by comparing model outcomes. Our analyses confirm that a high level of specialization leads to high sensitivity to habitat loss and fragmentation. When landscape quality is high, specialists are competitively superior, but when landscape degrades, generalists gradually become superior. In previous models, competitive hierarchy is usually thought to be an intrinsic property of species, but we show that a shift in competitive capacity is caused by extrinsic factors. Comparing deterministic versus stochastic models, we find that a key extrinsic factor is increase in demographic stochasticity in degraded landscapes that affects specialists more than generalists.

In the third chapter, I ask about the role of large-scale habitat corridor for biodiversity conservation. We analyzed a community of 300 species belonging to 6 taxonomic groups inhabiting more than 2000 km² forest, composed of two large national parks in Madagascar, Ranomafana and Andringitra, and connected by a corridor. We found that in 2000 the corridor was still functional, but since then it has degraded substantially and may lose its corridor function in the coming decades. Our spatially realistic simulations show that species with passive mode of dispersal suffer the most from corridor destruction.

This thesis emphasizes the role of different mechanisms that should be considered while analyzing species’ responses to changes in habitat structure. The most important ones are the mode of dispersal, ecological specialization, temporal and spatial stochasticity, and competition. As such, tropical regions, like Madagascar, are in double trouble due to high ecological specialization of most species and high rates of habitat destruction. Effective measures need to be enforced to ameliorate the conditions within and outside protected areas so they can truly enhance biodiversity protection.
Maro dia maro ny biby sy ny zavamaniry lany tamingana tao anatin’ny izay efa-jato taona lasa izy ary aman’alina no ahiana ho lany tamingana amin’ity taon-jato ity. Raha ny kajikajy dia efa ho avo arivo heny amin’ny tokony ho izy ny tahan’ny faharinganan’ny zavamanan’aina ankehitriny. Ny fianimana ny tontolo iaianana, indrindra ny tevy ala, atao’ny olombelona no antony voalohany mahaotanga izany faharinganan’ny zavamanan’aina izy. Ity asa ity dia mandalina misimisy kokoa ny voka-dratsin’ny fianimana ny ala voajanahary amin’ny ny zavamanan’aina monina ao anatin’ny ary miezaka ny mamantatra ny toetotron’ny biby na zavamanirhy ahiana ho ringana voalohany. Hanatrarana ny tanjona dia namorona sy namelabelatra fomba vaovao aho ahafana mandalina misimisy kokoa ny tahirinkevitra ary nandrafitra modely hanazavana ny fiovaovan’ny isan’ny mponina.


Ity asa ity dia mihezaka ny mamaritra ireo toetra tokony ho jerena manokana raha handanjalanja ny voka-dratsin’ny faharapahan’ny ala voajanahary. Ny tsy fananantsafidy amin’ny toerana iparitahana sy tsy fahabahanana mivelona amin’ny karazan-tsakafo sy toerana samihafa, ny fitasipatapin’ny sakafo, ary ny fitononanana eo amin’ny samy biby na zavamanirhy no fomitra voalohany mitarika ny faharinganana. Noho izany, anisan’ny tena ho sahirana i Madagasikara satria sady maro ny spesialisita no aho ny taham-paharipahan’ny ala. Mia miombozeka sy mandary andraikitra isika hiaro ny tontolo ianina anatin’ny sy ivelan’ny valan-javaboary mba tsy hahapotika ny harena sarobidy izay ananan’i Madagasikara.
SUMMARY

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PRELUDE

The term theoretical ecology is a difficult one to grasp. Based on personal experience, people are puzzled when I tell them: “I am a theoretical ecologist”. I believe the meaning is difficult to guess because of the seemingly conflicting connotations of ‘ecology’ and ‘theory’. Ecology is an empirical or even practical science dealing with organisms that can be seen, heard, and measured. In contrast, theoretical investigations, like mathematics, study abstract concepts, without obvious application to the real world. So before going any further, let me shortly clarify the apparent oxymoron.

To paraphrase Jonathan Losos, there is an analogy between a detective and a theoretical ecologist. The work of a detective consists of three phases: gather as much information as possible at the crime scene, analyze and make inference from that information, and validate the inference with additional evidence, for instance by finding the criminal. Likewise, the ecologist goes through those three phases but instead of crimes, the scenes are biodiversity patterns. An ecologist needs to collect data, formulate hypotheses, and validate them.

The second phase is usually verbal statements, and the difference between empirical and theoretical ecologist is the tools used for the third phase. Whereas an empirical ecologist gathers additional data, a theoretical ecologist tests the statement by using mathematics. More precisely, a theoretical ecologist translates the hypotheses into equations. The framework allows to substantiate and to test rigorously the verbal statement using the universal language of mathematics. The second phase is validated if the results of the equations and the original data match.

The analogy mentioned above extends: just as a detective tries to prevent future crime, so is an ecologist's duty to stop current loss of biodiversity. More data need to be collected, theories formulated and validated so that we have accurate knowledge of the causes of loss, and are able to implement appropriate action to conserve biodiversity. Because human well-being is dependent on proper functioning of ecosystems, reverting biodiversity loss is a priority and further values research conducted by ecologists.
1 Biodiversity patterns
Past to present

As far as space exploration goes, the Earth is the only planet with living organisms. The unusual conditions on the Earth, compared to extraterrestrial objects, supports and facilitates the proliferation of life. Prokaryote organisms like bacteria were present on Earth 4.2 billion years ago (Hedges and Kumar, 2009). Organisms with nucleus and mitochondrion emerged about 2 billion years ago. At present, there are 1.2 million described eukaryote species but there can be as many as 10 million species (Mora et al., 2011). In fact, Mora et al. (2011) estimated that more than 86% terrestrial species and 91% of marine species remain to be discovered.

Life on Earth has not always been a success story. In the past, large scale environmental changes interfered with the proliferation of life and caused the decline of many species. During the past 550 million years, five disturbances, caused by major geological events such as massive volcanic eruptions and impact of asteroids, wiped out most of earth’s diversity (Arens and West, 2008). For instance, 252 mya (million years ago), at the Permian-Triassic transition up to 96% of existing species went extinct (Benton and Benton, 2003). The fossil record suggests that only 0.1% of the species that have ever lived are still present nowadays (Raup, 1991). Nevertheless, mass extinctions also provide fresh opportunities for the emergence of new forms.

Anthropocene

The development of human civilization coincides with increased extinction rate. The losses started 50,000 years ago with the extinction of 90 genera of megafauna (greater than 44 kg) (Koch and Barnosky, 2006). During the past 400 years, more than 350 vertebrate and 400 invertebrate species have gone extinct (CBD, 2001, Chap. 1), and recent data suggest that the trend is accelerating. The last Living Planet Index (LPI) reported that since the 1970s, the sizes of 10,000 vertebrate populations (mammals, birds, reptiles, amphibians, and fishes) have become halved (WWF, 2014). The International Union for Species Conservation (IUCN) have classified 16,000 species as threatened due to their shrinking population sizes and geographical distributions. The IUCN assessment mostly considers well studied taxa like mammals, birds, and conifers and cycads, but additional data suggest that invertebrates and vascular plants are also highly threatened (Collen et al., 2012). In brief, the rate of biodiversity loss is about two to three orders of magnitude higher the background rate. If not halted, this will lead to the sixth mass extinction (Millennium Ecosystem Assessment, 2005).

Climate change occurred 10,000 years ago and caused the decline of the megafauna, but evidences suggest that human has triggered or precipitated their extinction. Growing human population interfered with other species by destroying natural habitats for agriculture, by depleting resources, and excessive hunting (Koch and Barnosky, 2006). These historical events are indeed perpetuated until present. Overhunting, overfishing, and illegal trade drive many species to extinction or to a dangerously low abundance. For instance, overhunting caused the extinction of great Auk in 1841 (Montevecchi and Kirk, 1996) and high demand for ivory has brought down the populations of elephants in Africa (Caughley et al., 1990). Overfishing almost depleted the population of Atlantic cod and the fishing has been closed indefinitely since 2003 (Millennium Ecosystem Assessment, 2005). In addition, deliberate or accidental introduction of nonnative species have caused 40% of historic extinctions (Krebs, 2001). The accidental introduction of brown tree snake in Guam in the 1950s drove extinct nine native species of bird (Engbring and Fritts, 1988; Fritts and Rodda, 1995). Nile perch introduced in Lake Victoria in 1980s drove 200 cichlid fish species to extinction (Seehausen et al., 1997).

However, the most visible effect of human activities is the extent to which humans have transformed natural landscapes (Fig. 1). Conversion of forest for agriculture, timber production and urbanization, creation of dams, agricultural runoff, and pollution (like oil spill) make the environment unsuitable for large numbers of species (Pimm and Raven, 2000). Box 1 explained three modes of habitat destruction. More than 70% of Mediterranean and temperate forest and 50% of tropical forest have been converted to agriculture. In fact, 70% of projected loss of terrestrial biodiversity will be caused by conversion to agriculture (CBD, 2014). The scale of habitat conversion makes it the principal threat to global biodiversity (e.g., Pimm and Raven, 2000).

So what?

The total number of existing species is hard to get a grasp of. There are so many of them so why can’t we lose a few or most of them? The truth is, our well-being is intricately linked with biodiver-
Figure 1: Forest loss between 2000 and 2012 in five continents. The size of the pie charts scales with the total amount of forest loss except for Australia, which has been magnified 10 times for visibility. Each pie chart shows the 3 most deforested ecozones (colors) and the rest (white). Source: Hansen et al. (2013)

Actions
Threats to biodiversity have received much attention in the past two decades and the severity of the biodiversity crisis has fostered global collaboration. In 1992 in Rio de Janeiro, the United Nation organized an international meeting called the Convention on Biological Diversity (CBD), which lead 94 parties (193 countries and the EU) to sign a treaty to conserve and sustain biodiversity (CBD, 2014). Because the principal cause of biodiversity loss is habitat destruction, one of the principal tasks is to combat that problem, as emphasized in a follow-up meeting in Nagoya, Japan (Aichi Target 11, CBD, 2010). The main solution is to increase the area of Protected Areas (PAs) which are expected to be safe from anthropogenic pressure, and buffer the respective populations and communities from the effect of habitat loss.

However, due to economical conflict and resource limitation, the extents of areas that can be protected are limited. Therefore, to have maximal impact, PAs should cover areas with high conservation value that contain large numbers of (endemic) species with high threat. The most important regions for conservation are called biodiversity...
hotspots (Myers et al., 2000). Although they cover only 1.4% of world’s land area, they contain 45% of vascular plants species and 35% of terrestrial vertebrate species. In 2003, PAs covered 11.5% of terrestrial and inland waters which surpasses the 10% goal set during Caracas congress a decade earlier. However, the vast majority of the protected areas lies at high latitude and elevations, which are not especially rich in biodiversity. The new target of protecting 17% by 2020 may be reached (CBD, 2014), but the key issue remains, how representative the PAs are of world’s most threatened ecosystems.

Box 1: Habitat loss and fragmentation

Habitat destruction may involve several causes including loss of habitat area (quantity), loss of habitat quality, and fragmentation of a given total area of habitat (Hanski, 2005).

Loss of habitat area represents a reduction in the total spatial extent of the habitat. Loss of quantity is quantified by measuring the area of the habitat before and after the loss. The panels on the left and right of the intact habitat in figure 2 are subject to habitat loss.

Loss of habitat quality is more complicated and does not necessarily relate to the spatial extent (Fig. 2). Moreover, loss of habitat quality is specific to the population or community of interest. For instance, the amount of wood debris in Finnish forest has declined from 120 m$^3$ ha$^{-1}$ in old growth forests to 4-10 m$^3$ ha$^{-1}$ in production and managed forests (Jonsson et al., 2005; Siitonen, 2001), which represents a drastic loss of forest quality for hundreds of decomposer species.

Habitat fragmentation has been measured in many different ways, taking into account patch sizes, number of patches, patch isolations, distance to the nearest patch and so forth (Fahrig, 2003; Wang et al., 2014) and there is no agreement on the best measure. The meaning of habitat fragmentation has been confusing and Fahrig (2003) recommended that fragmentation should only be used for situation where a given area of habitat is broken into several pieces independent of habitat loss and measured at a landscape level (Fig. 2, bottom panel). Hanski and Ovaskainen (2000) have derived a measure of habitat fragmentation at the landscape level, called the metapopulation capacity, from the metapopulation theory. This measure combines in a single value the effects of patch number, patch areas and their pair-wise distances (connectivities). In practice, habitat loss is accompanied by fragmentation and a pure case of fragmentation is only possible in experimental settings. Empirical examples of fragmentation (sensu Fahrig) include construction of dams and the construction of roads.

Collinge and Forman (1998) proposed four spatial patterns of habitat destruction called: bisection, perforation, fragmentation, and shrinkage (Fig. 2), which are caused by different human activities. For instance, bisection results from road construction, perforation from selective logging and mining, and shrinkage and fragmentation are caused by agricultural expansion.

![Figure 2: Patterns of habitat loss and fragmentation.](image)
Despite the success in increasing the total area of PAs, the principal goal to alleviate threats on biodiversity will most likely fail (CBD, 2014). The rate of extinctions have not been slowed down and the conservation status of species has worsened (CBD, 2014). There are three main reasons behind the failure of PAs. First, PAs do not cover high priority regions (Rodrigues et al., 2004; Cantu-Salazar and Gaston, 2010). For instance, the largest terrestrial PAs is Northeastern Greenland, and it covers almost 1 million km² but has low diversity. Second, conditions within PAs do not necessarily buffer population from extinction, because in many cases poaching, selective logging and deforestation are still common practices (e.g., Schwitzer et al., 2014). Third, many PAs are too small to sustain a viable population (Woodroffe and Ginsberg, 1998). More than 70% of terrestrial protected areas have an area of less than 10 km² (WDPA, 2009). Thus, even though some PAs harbor rich biodiversity, they can be too small and fragmented to support viable population.

An example: Madagascar

Madagascar has an exceptional high level of endemicism and high biodiversity, and it is classified as one of the most important biodiversity hotspots on Earth (Myers et al., 2000). More than 90% of plants, mammals, reptiles, and amphibians are endemic. Half of the chameleons in the world are found in Madagascar, and of taxonomic group like tenrecs, civets, and lemurs 100% are endemic. In fact, endemism in Madagascar is higher than in other biodiversity hotspots (Fig. 3) which makes Madagascar a perfect place to study the mechanisms that generate new species. The ancestor of many species groups in Madagascar arrived via overseas colonization after the last mass extinction at the end of Cretaceous (Simpson, 1940). Because mass extinctions free up ecological niches, they also create opportunities for new adaptive radiations. Adaptive radiation is an evolutionary process characterized by a rapid differentiation of species into an environment with many new ecological opportunities. Diversification rate eventually declines as species fill the ecological niches leaving fewer opportunities for further speciation (Schluter, 2000). Adaptive radiations are spectacular, because they produce large numbers of species and usually involve close association between the trait of the species and the environment.

Madagascar fauna and flora include many classic radiation of species, partly because of the diversity of environmental conditions it provides (Yoder et al., 2005; Wilme et al., 2006; Reddy et al., 2012). Madagascar is the fourth largest island (592,000 km²) and stretches for more than 1300 km from North to South. A mountain range, steep on the east and shallow on the west, generates complex topographical landscape and contrasting climate between the East and the West of the island. In addition, Madagascar has been isolated for more than 88 my (million years) leaving plenty of time for evolutionary processes to operate.

Dung beetles is an example of successful radiations in Madagascar with 300 species which 96% are endemic In comparison, Borneo and New Guinea have 120 each, of which 83% and 38% are endemic (Writa, 2009). Malagasy dung beetle fauna is the result of eight independent colonizations in the past 50 to 70 my (Miraldo et al., 2011). The most recent radiation, consisting of the genera Nanos-Apotolamprus (NA) is particularly speciose (74 species) and it has had twice the rate of net diversification in comparison with other dung beetles radiations in Madagascar (Wirta et al., 2010). Due to high resource competition in the dung beetle communities (Hanski and Canbefort, 1991), they are ideal for studying the role of competition and range dynamics in species evolution (Miraldo and Hanski, 2014).

Sadly, biodiversity in Madagascar is also highly threatened by habitat destruction, mainly slash and burn agriculture. During the last 50 years, forest cover has declined by almost 40% (Harper et al., 2007). Blocks of forest greater than 10,000 km² in area used to constitute 60% of the total forest cover 50 years ago but has been reduced to only 16%. At the same time, forest fragments less than 10 km² in area increased from 5% of the total forest area to 24%. The highest loss has occurred within pristine forest (Hansen et al., 2013). Such dramatic decline in forest cover elevates the threats on biodiversity. Altogether, 116 mammals, 35 birds, 135 reptiles, 69 amphibians, 86 fishes, 24 mol-lusks, and 86 other invertebrates and 374 species of plants have been listed as threatened in Madagascar (IUCN, 2014). It is particularly alarming that 96% of the 103 lemur species (Schwitzer et al., 2014) and 80% of the 192 palm species are threatened (IUCN). More than 90% of Malagasy fauna and flora are forest specialists which makes them particularly vulnerable (Dufils, 2003).

The peril of Malagasy fauna and flora is well known and major conservation actions have been implemented. Following the announcement dur-
ing the World Park Congress (WPC) in Durban in 2004 by the former president Marc Ravolomanana, the total area of PAs was tripled to cover 10% of the territory (Gouvernement Malgache, 2004). A forest corridor between Ranomafana and Andringitra National Parks, located on the South Eastern escarpment of Madagascar, was targeted for conservation action. This corridor stretches for 95 km with width varying between 2 and 50 km. The corridor and the parks host more than 800 species of plants and 300 species of vertebrates and is home of the Critically Endangered larger bamboo lemur *Prolemur simus* (IUCN, 2014). In addition, the area is a major source of fresh water, with sources of 25 rivers and about 166,000 people depend on the forest and revenues from the national parks (Conservation International, 2014).

2 **Theories**

The sections above described patterns and threats to biodiversity especially in Madagascar. The sections below focus on the mechanisms that influence the origin and persistence of biodiversity.

**On the origin of species**

In 1859, Darwin proposed a theory that would change the world (Darwin, 1859). The theory suggested that no species appear instantaneously in the course of history but the species are instead derived from the existing one. New species are the consequence of gradual modifications of their physiological, behavioral, and ecological traits by natural selection. Eventually, the original and the derived traits have diverged so much that the new form has become a separate species. This process, called speciation, gives rise to all organisms that have existed and exist today. The theory is a key break through if not the most important discovery in natural science.

New scientific question emerged from Darwin’s formidable insight. Large numbers of studies have attempted to explain particular mechanisms of divergence. Species can diverge after being separated by physical barrier leading to allopatric speciation, which is believed to be the dominant mechanism of speciation (Coyne and Orr, 2004). Sympatric speciation has been much debated and although some empirical evidences are now available, sympatric speciation is considered an uncommon form of speciation. Modern synthesis focuses on the underlying mechanisms of different modes of speciation, such as the role competition, evolution of reproductive isolation, reinforcement, changes in genetic architecture, and so forth (Butlin et al., 2012).

Darwin’s theory implies that every pair of species has a common ancestor if one goes far back in time. Thus, another central question is to reconstruct the phylogeny for species of interest (Box 2). Phylogenetic inference assumes that the more recent the divergence, the more similar the species are. In the past, similarity was inferred from morphological traits but has now been complemented by molecular data. Since the ‘molecular revolution’ and the use of molecular data in phylogenetic inference, the number of studies have increased exponentially (Pagel, 1997), with 15 new trees are published on average every day (Rokas,
Phylogenetic inference has become one of the most active fields in evolutionary biology. Not only do phylogenies describe relatedness of species but may contain clues about mechanisms of speciation (Harvey and Pagel, 1991). For instance, the pattern of relatedness (topology of the tree) can be informative about the geographical mode of speciation. For instance, the phylogeny of cichlid fish in the Crater Lake Apoyo in Nicaragua reveals that species within the lake are more closely related than species between lakes. The monophyletic origin of species within the lakes strongly suggests that speciation has occurred sympatrically, without (obvious) geographical barriers (Barluenga et al., 2006).

**Box 2: Introduction to phylogenetic tree**

A phylogenetic tree or phylogeny is a graphical representation, like a family tree, of evolutionary relationship in a group of species. Linnaeus was the first to classify species based on their degree of resemblance (Linnaeus et al., 1758) but since he had no concept of evolution, the grouping was simply a practical way of classifying species. However, there is no way of knowing exactly how different species are related to each other and a phylogeny is only a hypothesis, the results of statistical inference. The original data for the construction of a phylogeny consist of a single matrix, in which the rows represent the set of species and the columns represent morphological, behavioral traits, and nowadays more commonly DNA sequences. There are four main methods to construct (more precisely to infer) a phylogeny: parsimony methods, distance-based methods, maximum likelihood methods, and Bayesian inference. These methods search for the tree that represent the minimal number of evolutionary changes that gave rise to the extant species.

A phylogeny has three components. The final nodes, tips, or leaves (Fig. 4, red dots) represent the extant species whose relatedness have been inferred. The internal nodes (Fig. 4, black squares) represent branching (speciation) event, at which points sister species are formed. Sister species are derived from the ‘mother’ species, the most recent common ancestor, which is different from relatedness in human genealogy because the mother can be one of the sister species.

There are three types of trees depending on the interpretation of the branch length (Fig. 4). In the simplest case, the branch length has no meaning and the tree is called a cladogram. Cladograms are used to visualize the relationships among species. When the branch length represents time, the tree is called a chronogram, an ultrametric tree, or time-calibrated tree, where the internal nodes represent the estimated times of speciation. When the branch lengths represent evolutionary steps, the tree is called a phylogram. For cladograms and chronograms, the branches connecting sister species to their most common ancestor always has the same length.

Because phylogenetic trees are the outcome of statistical inference, the resulting trees are subject to uncertainty with respect to the topology (relatedness among the species) and the branch lengths (the timing of speciation in ultrametric trees). Each internal node can be associated with a value that represents the degree of confidence about the relationship between the sister species, while a horizontal bar showing the confidence about node age.

![Figure 4: Three types of phylogeny.](image-url)
With the vast amount of data and phylogenies, more specific questions can be asked which has led to the development of new methods for inferring the mode and tempo of evolution. One of the more sophisticated methods is a group of statistical models called the State-Speciation-Extinction model (Stadler, 2013). The idea is to find correlation between the tempo of evolution (e.g., speciation, extinction, trait changes) and the traits themselves. For instance, one can ask whether large animals are more likely to speciate than small ones (Rabosky, 2014). The correlation may provide hints on the effect of the traits on diversification rate.

Inferring the effects of geography on species diversity is indeed to primary goal of the Geographic State-Speciation-Extinction (GeoSSE) model (Goldberg et al., 2011). The GeoSSE assumes that speciation, extinction, and colonization rate from one region to another are region-dependent. It uses likelihood approach to understand if extant diversity is explained by differences in speciation, extinction, or colonization. For instance, the model has been used to explain latitudinal gradient in mammalian diversity (Rolland et al., 2014). The authors concluded that the tropical regions have more mammals than temperate regions because speciation rate is higher in the tropics. The GeoSSE model is one of the first macroevolutionary models that combines inference of range dynamics with extinction and speciation dynamics. Unfortunately inference in this model is limited to only two regions.

**Population response to habitat loss and fragmentation**

Species have evolved to be well adapted to particular environments, but they are often pushed outside of their niches as habitats are modified. Below, I summarize what is known about species’ responses to habitat loss and fragmentation.

Habitat loss alone has a direct negative effect on population size. The realized population size is a function of energy available and the population size will be reduced if the amount of available energy is reduced. In contrast, habitat fragmentation (sensu Fahrig, Box 1) can both harm or benefit a population. When competition is distance-dependent, increased fragmentation lessens the intensity of competition and consequently increases population size (e.g., North and Ovaskainen, 2007). Species adapted to use habitat edges (e.g., edge-inhabiting predators, Ambuel and Temple, 1983) can benefit from increased amount of edges in fragmented landscape. Finally, isolated habitat fragments may act as refuges if spatially correlated environmental stochasticity wipes out the populations from a large part of its range (Quinn and Hastings, 1987; Wissel and Stocker, 1991; McCarthy et al., 2005; Ovaskainen, 2002).

In most cases, habitat loss and fragmentation are entangled and their negative effects generally outweigh the aforementioned potential advantages (North, 2010). The theory of Island biogeography (MacArthur and Levins, 1967) and metapopulation theory (Hanski, 1999) emphasize the importance of both the amount of available habitat and landscape configuration for population and community dynamics. In short, species occupying small and isolated habitats have a greater risk of going extinct than populations occupying large and well connected habitats. Further, small and isolated habitats are less likely to become colonized than large and well connected habitats.

However, not all species are equally vulnerable to fragmentation, but sensitivity to habitat loss and fragmentation depends on the traits of the species (Henle et al., 2004). For instance, species with small natural population size are more prone to extinction simply because they are closer to extinction. One trait that strongly correlates with low population size is high ecological specialization. When the initial distribution of niche is narrow, chances that the entire niche space will be wiped out due to habitat loss is high. The ability to stabilize population size when facing environmental perturbations is key for persistence (Henle et al., 2004). Large fluctuations in the environment can bring a population to extinction or to a small number. Some species are able to tolerate harsh environmental conditions due to the storage effect which refers to the ability to survive harsh conditions by using resources stored during favorable periods (Chesson, 2000b,a; Snyder and Chesson, 2004). The mechanism will buffer population and prevent it to reach dangerously low level. Other traits like body size, trophic position, sociality and reproductive potential have been suggested to be related to high risk extinction, but there is no conclusive evidence to draw general conclusions (Henle et al., 2004).

The ability of species to disperse across landscape is essential for species that face local frequent extinctions and thus need to recolonize empty habitat patches (Clobert et al., 2012). However, dispersal ability does not necessarily correlate with sensitivity to habitat loss and fragmentation. For instance, Fahrig (1998) used a spatial explicit sim-
ulation model to show that species with intermediate dispersal capacity suffer most from fragmentation. Because spatially autocorrelated environmental stochasticity might elevate extinction risk of species with short dispersal range, large dispersal range is thus often thought as a way to escape from the negative effects of fragmentation.

It is natural to ask when habitat loss becomes so severe that a species is no more able to survive? The tipping point between persistence to extinction is called the extinction threshold. In the same landscape, one species with high dispersal capacity might be able to exploit isolated patches while another species with short dispersal capacity might be trapped in a single patch and thus have more limited resource availability. Thus, the extinction threshold is not only a function of the landscape but depends also on species-specific traits.

Population size does not necessarily change proportionally with the degree of the habitat destruction. When population size decreases, mechanisms such as the Allee effect (Stephens and Sutherland, 1999; McCarthy, 1997) or inbreeding depression (Lande, 1993; Saccheri et al., 1998) becomes important and can create a non-linear effect. The joint effect of such forces in reducing population size has been called the extinction vortex, and it can lead to population collapse even after a minor change in the environment. The consequence of such nonlinearity is that extinction threshold is reached even when some habitats still remain (Tilman et al., 1997; Hanski and Ovaskainen, 2000).

Growth, dispersal, and even mortality take time creating a time lag before observing the eventual effects of habitat loss and fragmentation. The delay between the time when habitat destruction occurs and the time when the population size reaches a new equilibrium is called transient time (Hanski and Ovaskainen, 2002). During the transient time, the species may still occur in the landscape even though the extinction threshold has been crossed. Such species are doomed to extinction but they have not yet time to go extinct. The number of species that will eventually go extinct but still persist is called the extinction debt (Tilman et al., 1994; Hanski et al., 1996).

Community response to habitat loss and fragmentation
It would be of great practical value to be able to predict the fraction of species that will be lost due to a given degree of habitat loss and fragmentation. The Species Area Relationship (SAR) is one of the most consistent pattern in ecology. As the SAR describes how many species are expected to be found in a given area, it can be used to estimate the number species lost after a certain degree of habitat loss. SAR says that at logarithmic scale, the number of species found from an area increases linearly with the size of the area with a proportionality constant $z$ (Arrhenius, 1921). As the SAR describes how many species are expected to be found from in a given area, it can and therefore is used to estimate the number species lost after a certain degree of habitat loss (Whitmore et al., 1992; May et al., 1995; Cowlishaw, 1999; Pimm and Raven, 2000; Brooks et al., 2002; Brooks and Balmford, 2003; Pereira and Daily, 2006; Pimm et al., 2006; Hanski et al., 2007). There has been much debate on the applicability of SAR i.e. whether it over-estimates or underestimates species loss (He and Hubbell, 2011; Rybicki and Hanski, 2013). As a consequence, more refined models have been built to account for factors ignored by the basic SAR models, such as the spatial distribution of species (Kinzig and Harte, 2000; He and Hubbell, 2011; Rybicki and Hanski, 2013). These studies have shown the value of the parameter $z$ depends on the spatial scale of the study, on the aggregation level of the species’ distribution, whether landscapes are contiguous or fragmented, and whether the focus is on immediate or long term extinction.

At a community level, species interactions such as predation, mutualism, and competition will propagate the effects of habitat loss and fragmentation. Different species have different sensitivities to habitat destruction, and the decline of one of them will influence also the others, either positively or negatively. One of the most studied interaction types is competition, especially the coexistence within guild (reviewed in Box 3). In a community structured by a competition-colonization trade-off, Tilman et al. (1997) showed that species with low colonization ability (high competitive ability) may suffer most from habitat destruction. As the landscape deteriorates, the relative abundance of the competitively inferior species initially increases. Such a pattern has been observed empirically for generalist and specialist species but the underlying mechanisms are still poorly understood (Jonsen and Fahrig, 1997; Nordén et al., 2013; Gibbs and Stanton, 2001; Conole and Kirkpatrick, 2011). More theoretical work is thus needed to identify traits that make species especially sensitive to habitat alteration and to understand the mechanisms behind extinction processes.
Theory and conservation
As mentioned above, current PAs are not large enough and often also not optimally placed to preserve biodiversity. For future PAs, there are various algorithms available to help select the best areas. For instance, the software package Zonation uses a series of algorithms to select the most representative areas based on predefined constraints such as cost, land-use, species interaction and so forth (Moilanen et al., 2014). For existing PAs, one approach is to increase the core area and thus minimize the negative effect of habitat loss. Another approach is to increase connectivity between PAs and thus minimize the adverse effects of habitat fragmentation.

Creating corridors between PAs is a popular measure for biodiversity conservation, at least on paper. Corridors are thought to facilitate movements and to increase the persistence of population in habitat fragments that they connect (e.g., Beier and Noss, 1998). They can be defined as habitat corridors, movement corridors or stepping stone corridors but the ultimate goal is to reduce the negative effect of isolation by connecting previously isolated areas. In addition, corridors provide additional habitats and thus can be valuable for biodiversity conservation.

In practice, however, not much evidence supports the efficiency of corridors, and debates remain whether other measures should be implemented (Simberloff et al., 1992; Haddad et al., 2014). Empirical work on corridors has usually been conducted on small spatial scale, using small-bodied organisms of little importance for conservation (e.g., Forney and Gilpin, 1989; Gonzalez et al., 1998; Damschen et al., 2006). For instance, Gonzalez et al. (1998) found that a 7 cm long moss corridor has a positive effect on population density of microarthropods. Extrapolating such results to large spatial scale and to conservation planning is problematic. Furthermore, empirical testing of the influence of large scale corridor would be very time consuming because of long transient time and logistics constraints. In many cases, lack of appropriate replicates prevents evaluating the differences between isolated and connected patches (Gregory and Beier, 2014). However, several biodiversity hotspots need conservation actions in which improving the performance of PAs is an urgent task. Therefore, it is important to consider the existing theories and models about species’ response to habitat loss and fragmentation and how they could be used and modified to infer the importance of large scale corridors for species’ persistence.

Aims of the thesis
Landscape heterogeneity plays a key role in shaping population, community dynamics, and up to clade evolution. Since studying all communities is impossible, there is a need to draw general knowledge on the feedback between physical property of the landscape and species traits. Such knowledge can be obtained from theoretical models, these results of which should be evaluated with real ecological communities.

The overall aim of this thesis is to combine theoretical and empirical works to assess the importance of spatial processes in evolution, ecology, and conservation. The first specific goal is to make inference on the role of spatial heterogeneity for lineage diversification and the dynamics of geographical ranges (I). The second goal is to understand how species with different levels of specialization respond to habitat destruction (II, III). Whereas the aim of Chapter II is to gain general insight, Chapter III focuses on an actual case study in Madagascar.

Combining theoretical and empirical works can be challenging. The simplicity in model assumptions adopted by theoretical models is often in contrast with the complexity of real biological systems. There is a need to find middle grounds that bridge the two worlds. From a mathematician point of view, we constructed models that incorporate a myriad of biological assumptions (II). From an empiricist point of view, we constructed models that are either gross simplification (II) or tailored to address a conservation problem (III). The specific goals of each chapter are:

Chapter I: to assess the simultaneous effects of range dynamics and rates of speciation and extinction on diversity. To achieve this, we extend the GeoBSE approach to allow inference for multiple regions and by assuming that diversification rates are diversity-dependent. We apply the method to understand the evolutionary history of Malagasy dung beetles and thus to provide insight about the origin of biodiversity in Madagascar.

Chapter II: to understand the coexistence of species with different niche width, and how niche width influences the abundance and persistence of the species for different intensities of habitat loss and fragmentation. To achieve this aim, we construct a general model for communities of generalist and specialist species in a heterogeneous landscape. The model is used to provide general insight about the role of life-history, competition, demographic stochasticity, dispersal, and density and distribution of resources for species persistence.
Chapter III: to evaluate the importance of the 95 km long corridor that connects Ranomafana National Park and Andringitra National Park in enhancing the protection of biodiversity. We investigate the quality of the corridor at present and how future deforestation will influence the persistence of generalist and specialist species in the parks.

3 Material and Methods

Most of the work in this thesis is based on mathematical and statistical models. We do not collect new datasets but use existing ones to build up mathematical models that mimic population and community dynamics. The rigor that is intrinsic to mathematics serves on one hand to verify or falsify verbal hypotheses and ecological theories by comparing the outcomes of the models to empirical patterns, and on another hand to make predictions that can be tested in the field or the laboratory. Mathematical models are simplifications of real ecological systems and as such they are useful for obtaining a general understanding of the system under study. In modeling, the most critical part is to find the balance between ecological realism and mathematical tractability.

To model dynamics through time, most mathematical models assume that the future state only depends on the present state of the system and thus not on its past states. For instance, the size of the population for the next generation is assumed to depend only on the size of the current generation. Such assumption is modeled by first order difference and differential equation. Mathematical models can be classified into discrete or continuous time, spatial or non spatial models, deterministic or stochastic models, and so on. In this thesis we model stochastic processes with Markov chains (III) or Markov processes (I, II). Box 4 defines and shows how to simulate these processes.

Modularity. There are several classes of models for the same research questions and the choice among different model types is often based on the modelers preferences. In some cases the different model classes give different predictions which can be compared to provide additional insight into the question in hand. For instance, comparison between deterministic and stochastic model can be used to assess the influence of stochasticity for small populations. In Chapter II, we built an integrative framework so that mechanisms can be added or removed. Therefore, we can investigate the marginal and joint effect of different mechanisms by comparing the outcomes of the models.

In total, we evaluated 28 model variants.

Space. Because the main goal of the thesis is to understand the influence of spatial processes, all chapters included explicit representations of landscape structures (Fig. 5). To investigate the effect of regional differences on diversification rates in Madagascar (I), we divided the island into five regions (Fig. 5a). These 5 regions are based on topographic and climatic differences, and the same classifications were also used to study the biogeography of dung beetles in earlier study (Miraldo and Hanski, 2014).

To investigate the effect of habitat loss and fragmentation on species diversity, we considered both simulated (II) and actual landscapes (III). In Chapter II, we used simulated landscapes (Fig. 5b) which enabled us to control separately the effect of habitat loss and fragmentation. We increased fragmentation (sensu Fahrig) by shrinking the size of the patches (circle) but keeping the density of resource units (dots) within each patch constant. We increased habitat loss by lowering the density of resource units within the patches but keeping patch sizes constant. The colors represent different types of forest or resource unit (e.g., birch, pine, spruce).

In Chapter III, we used actual forest cover for Ranomafana-Andringitra corridor (Fig. 5c) modified from Hansen et al. (2013). We simulated habitat destruction in the corridor by gradually converting forests to non-forests. Deforestation was assumed to propagate from non-forest areas by letting a cell has higher chance to be converted to non-forest if it is surrounded by non-forests. The rate of conversion was estimated from the observed change in forest cover between the years 2000 and 2012.

Dispersal. We used three types of dispersal. In Chapter I, dispersal occurs to the nearest neighbor (Fig. 5a). Because very few dung beetles occurred in the central part of Madagascar, and because the goal was to apply the model to a community of Malagasy dung beetles, we did not allow dispersal from West to East and vice versa. In Chapters II and III, we assumed a distance-dependent dispersal kernel. In Chapter II, we used a passive dispersal with a top-hat dispersal kernel. In Chapter III, the dispersal kernel is more realistic as it consists of a Gaussian dispersal kernel. In addition, we explored the dynamics under three modes of dispersal: passive, active without gap-avoidance and active with gap-avoidance. With gap-avoidance, the propagules are assumed to not be able use non-forest as their dispersal routes.
Figure 5: Landscape structures assumed in this thesis. c) Ranomafana (Andringitra) National Park is located in the northern (southern) part of the map and shown by green color. Observed forest cover in the corridor in year 2012 is shown by black and gray colors. Cells shown in gray will be cleared after 50 years according to our simulation. Stars represent sites where the corridor is narrow (less than 1 km).
Table 1: Summary of models used in each chapter

<table>
<thead>
<tr>
<th>Event</th>
<th>Coexistence of generalists and specialists (II)</th>
<th>Effectiveness of habitat corridor (III)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>- Continuous</td>
<td>- Discrete</td>
</tr>
<tr>
<td>Space</td>
<td>- Discrete space (Fig. 5a)</td>
<td>- Satellite based forest cover (Fig. 5c)</td>
</tr>
<tr>
<td>Dispersal</td>
<td>- Passive</td>
<td>- Top-hat dispersal kernel</td>
</tr>
<tr>
<td>Fitness</td>
<td>- N.A.</td>
<td>- Niche width influences fecundity or establishment</td>
</tr>
<tr>
<td>Event 1</td>
<td>- Speciation (within or between regions)</td>
<td>- Birth of resource of a given type as a function of landscape quality</td>
</tr>
<tr>
<td>Event 2</td>
<td>- Extinction is diversity-dependent and causes range contraction or extinction if endemic</td>
<td>- Resource units are removed at random causing mortality for the species occupying the resource unit</td>
</tr>
<tr>
<td>Event 3</td>
<td>- Colonization only depends on patch connectivity (Fig. 5a)</td>
<td>- Colonization depends on fitness, dispersal, and competition</td>
</tr>
</tbody>
</table>

**Generalists versus specialists.** We defined a generalist species by its ability to exploit a whole range of resource types whereas a specialist species is limited to a narrow range of resource types. We assumed that there is a trade-off between breadth of resource types use and efficiency. Therefore, a specialist has a higher performance than a generalist in its optimal resource type but lower than the generalist otherwise. Specialist species’ efficiency can be expressed by high fecundity rate (II), by high establishment rate (II), or by high colonization and low extinction rate (III).

**Statistical models.** In Chapter I, we developed an extension of current phylogenetic comparative method. Instead of the maximum likelihood approach used in SSE-models, we inferred region specific speciation, extinction, and colonization rates using Approximate Bayesian Computation (ABC). The underlying macroevolutionary process is called Geographic Radiation (GR) and is described in Table 1. The shift to ABC allowed us to include additional assumptions that would be very difficult to solve using the maximum likelihood approach. Box 5 describes the basic principles of ABC.

**Data.** In Chapter I, we analyzed the phylogeny and distribution of the Nanos-Apotolamprus clade (Fig. 6). In Chapter III, we compiled and analyzed community data for Ranomafana and Andringitra published by Goodman and Razafindratsita (2001). These data were obtained from surveys between 1993 and 2000 at 3 sites in Ranomafana NP, 4 sites in Andringitra NP, and 8 sites in the corridor. There are over 300 species belonging to 5 taxonomic groups: lemurs, small-mammals, birds, amphibians, and reptiles. Forest cover by Hansen et al. (2013) was classified into intact forest if canopy cover is over 96%, degraded forest when canopy cover is between 68% and 96%, and the rest was assumed to be non-forest.

4 Results and discussion

**Phylogenetic comparative method**

Phylogenetic trees may contain many kinds of signatures of evolutionary processes (Harvey and Pagel, 1991; Statler, 2013). A vast number of phylogenetic trees are nowadays available, and a myriad of phylogenetic comparative methods have been developed to address different kinds of questions about the tempo and mode of evolution. The
first part of this thesis extends the GeoSSE (Goldberg et al., 2011) model by allowing inference for multiple regions and by assuming that diversification rates are diversity dependent. Because of the diversity-dependence, the usual likelihood-based approach becomes intractable. As a remedy, we adopted the ABC method for parameter inference.

Our method could not estimate simultaneously within-region speciation, extinction, and colonization parameters. This is because the model cannot detect if e.g. a high regional diversity is caused by high rate of speciation or low rate of extinction. If we fixed either within-region speciation or extinction parameters, the model was able to reliably estimate the remaining parameters. Thus, the Geographic Radiation (GR) model can be used to compare net diversification rates among regions and thus extends the GeoSSE, which is limited to two regions.

We applied the GR to the phylogeny of Nanos-Apotolamprus (Fig. 6) to compare net diversification rates among regions by assuming that either within-region speciation or extinction rates are equal. When extinction rates were fixed, within-region speciation rate was estimated to be highest in the North, and lowest in the West. The dissimilarities among regions were even more pronounced when speciation rates were fixed and extinction rates estimated. In this case the extinction rate was clearly lowest in the North and highest in the West (Fig. 7, rightmost column).

The northern part of Madagascar has heterogeneous environmental conditions due to complex topography. Such conditions are likely to buffer species against extinctions, even during long periods of changing climatic conditions because species are always likely to find conditions suitable for them. In contrast, the western part is relatively flat and dry. Despite being the largest in surface area, our results suggest that the effect of area is not sufficient to promote a high rate of diversification. Instead, our results suggest that for Malagasy dung beetles, diversification rates correlate with landscape heterogeneity.

We estimated that for Nanos-Apotolamprus colonization rate is of the same order of magnitude as the extinction rate. This result indicates that, for dung beetles in Madagascar, range expansion can be relatively slow. Due to resource limitation, the community of dung beetles is highly competitive (Hanski and Cambefort, 1991), which likely limits the geographical distribution. For instance, Viljanen (2009) found that some species have very narrow ranges, with little overlap with other species in their altitudinal distributions. Theoretical studies have shown that competition can play a significant role in range evolution and can easily limit species range (Case and Taper, 2000; Price and Kirkpatrick, 2009). Although we can only make hypotheses about the underlying mechanisms behind the slow range dynamics, our results provide an example of ecological dynamics that in-
Figure 7: Performance of the GR with simulated and empirical data. The first column compares true value against the mean of the approximated posterior distribution for simulated data. The second column shows the approximated posterior distribution for the empirical data (Fig. 6), conditional on the extinction rate being fixed. Based on the same empirical data, the third column shows approximated the posterior distribution, conditional on the within-region speciation rate being fixed.
influences evolutionary processes at an evolutionary time scale.

How much can we learn from phylogeny?
The main setback of the model is the inability to jointly infer within-region speciation and extinction rates. The problem is seen as a strong posterior correlation between these parameters. In other words, the same level of regional species richness can be obtained with different values of extinction and speciation rates as long as their ratio is equal. Pervasive correlations between parameters have already been pointed out by Goldberg et al. (2011).

In the two-region model GeoSSE, Goldberg and her co-author found a correlation between extinction and colonization rates, but this did not hamper the joint estimation of regional speciation, extinction, and colonization rates. In our five-region system, the problem is severe enough to preclude joint estimation of these rates independently.

Another problem that might limit the power of the GR is the use of ABC instead of the exact likelihood approach. Although ABC permits the parameterization of the complex macroevolutionary model, the trade-off is a possible loss of information. Theory shows that the posterior distribution approximated by ABC converges to the true posterior distribution when the summary statistics are sufficient. However, in most of the cases, such statistics might not be easy to derive or might not even exist. In the GR, we tested many possible summary statistics that we considered relevant from the biological or statistical points of view. In the end, only four summary statistics were informative: the total number of species per region, the distribution of the range of the species, the difference between the distributions of sister species, and phylogenetic diversity. These statistics do not capture all the possible information in the phylogeny, for instance branch lengths and the topology of the tree. However, the strong posterior correlations that precludes accurate inference on individual parameters is not necessarily caused by the ABC approach. The same issue was found in the GeoSSE model parameterized using a full likelihood approach (Goldberg et al., 2011). Future work is needed to quantify how much information is lost when one switches from a full likelihood model to the ABC model for comparative phylogenetic inferences.

The GR was not successful for estimating between-region (allogentic) speciation rate and the initial range of the last common ancestor. We suggest that these cannot be estimated because there is not enough information in the data. For example, when dispersal rate is high, historical information about ancestral range becomes unreliable. More specialized biogeographic models for ancestral reconstruction like the Dispersal-Extinction-Cladogenesis model by Ree and Smith (2008) have been extensively used to reconstruct ancestral ranges. However, those models only work when rates of change in species’ ranges are low compared to rates of cladogenesis. Estimating between-region speciation rate is particularly difficult for multiple regions due to the large number of ways the ranges can be partitioned.

Caveats
Although the GR is quite sophisticated, it makes some key simplifying assumptions. First, while GR allows extinction and within-region speciation rates to be diversity-dependent, we did not use the same functional forms as in previous studies (Rabosky and Lovette, 2008; Etienne and Hageeman, 2012). This is because those forms had more parameters than with our model, which we attempted to keep as simple as possible. Second, we assumed that diversity-dependence only influences within-region speciation and extinction rates. In reality, colonization rates can also be diversity-dependent. For example, when all niche space is utilized, not only diversification slows down but also there are less resources available for colonization. Third, we assumed that the environment remains constant in time and in space, which assumption was surely violated over the evolutionary period considered in our study. For instance, climatic conditions have waxed and waned forest cover in Madagascar creating conditions for allogentic speciation during times of forest retreat (Wilme et al., 2006). These assumptions and many more could be implemented into our model, at least in principle, but incorporating more processes and parameters would most likely further increase uncertainty in parameter estimates.

Influences of niche width and life-history on population dynamics
In Chapter I, we found that environmental heterogeneity can promote diversification and higher level resource use specialization. Chapters II and III evaluate the consequences of specialization for population and community dynamics. For brevity, I use interchangeably specialists for species with specialized resource use and generalists for species with generalized resource use.

High level of specialization can limit geographi-
The second question we asked is whether specialist species have higher extinction threshold than generalist species, and if so, what makes specialists more sensitive to habitat availability. In Chapter II, we found that without demographic stochasticity, extinction threshold only depends on mortality rate and background colonization rate. In fact, extinction threshold does not depend on establishment, fecundity, nor niche width. Generalist and specialist species have the same extinction threshold (II).

In contrast, when we add spatial and stochastic processes, the extinction thresholds for both the generalist and specialist species are higher (Fig. 8, dots in left panel). However, the specialist species reach their extinction threshold earlier than the generalists. The result is in line with many empirical studies that found that specialists are more vulnerable to habitat loss and fragmentation (Henle et al. 2004). A simple explanation is that as landscape deteriorates, the specialists experience more stochasticity in their resources. As the variance of demographic stochasticity increases, growth rate decreases (Lande et al., 2003). Interestingly, specialist species have the same the extinction threshold both in the establishment and fecundity models.

We also looked at the effect of dispersal range on species persistence. The ability of species to disperse across landscape is essential for species that face frequent local extinctions and thus need to recolonize empty habitat patches (Clobert et al., 2012). In general, high dispersal ability is considered to facilitate the persistence in fragmented landscapes (e.g., Fahrig, 1998). However, the optimal dispersal strategy depends on the pattern of fragmentation (Fig. 9). In Chapter III, we found that increasing dispersal range leads to a lower occupancy but only for passive dispersers. When landscape is severely fragmented, long dispersers not only lose more propagules in the matrix but have fewer propagules colonizing nearby sites. For active dispersers, no propagules are lost and dispersal range correlates positively with occupancy (Fig. 9).
Influences of interspecific competition on community dynamics

The results above were obtained assuming no interactions between the species. In Chapter II, we extended the fecundity and establishment models to investigate the influence of species interactions for population dynamics. The first question to ask in community ecology is about coexistence. For example, under which kinds of conditions generalists and specialists are expected to persist if they compete for the same resources?

For the establishment model, coexistence depends on two variables: the relative rates of propagule production by the specialists and generalists, and the amount of overlap between the specialist species. When specialists produce more propagules than the generalists and their overlap is not too strong, coexistence is possible. Although this mechanism is intuitive, it has not been included in earlier models that explored coexistence between generalist and specialist species, as those models assumed that generalist species are always inferior to specialist species in their competitive ability (Wilson and Yoshimura, 1994; Abrams, 2006). These earlier models have assumed discrete and finite types of resources, and that each resource type is associated with one specialist. In contrast, our assumption of continuous variation in resource type allows for a less strict niche overlap among generalists and specialists. Imperfect specialization is more than likely in real system. Based on our results, these imperfections facilitate coexistence among species with different niche widths.

For the fecundity model, no stable coexistence is possible under the deterministic model. When all the parameters are equal but niche width, the system follows a zero-sum dynamics meaning that the total abundance is fixed but the relative proportion of species is random (Brown, 1981; Hubbell, 2001). If the strict equality is broken, say the total amount of propagules produced differ, the species with the highest amount of propagules will exclude the others. Coexistence in fecundity model requires additional mechanisms, such as spatial segregation and demographic stochasticity (II). Our results agree with earlier findings showing that some forms of environmental variation is required for a generalist to persist in a community involving a set of specialists (Box 3, Wilson and Yoshimura, 1994; Abrams, 2006).

As mentioned in the section above, demographic stochasticity harms the specialists more than the generalists. Thus, when we move from deterministic to stochastic model, the generalists gain advantage and may outcompete the specialists. The exclusion by the generalists is more likely as the environment becomes more random. Nagelkerke and Menken (2013) questioned the ubiquity of specialist species. We suggest that for stable coexistence, at least an additional mechanism is required that favors the specialists. One additional mechanism is resource type aggregation (II). From the point of view of the specialists, resource type aggregation removes the fluctuation in the availability of resource types thus dampens the effect of demographic stochasticity. Recently, Buchi and Vuilleumier (2014) came to the same conclusion that increased spatial autocorrelation in environmental conditions benefits the specialist species.

Empirical studies have found that as habitat quality deteriorates e.g. due to anthropogenic disturbance, the relative abundance of generalist species may first increase and then peak at an intermediate level of disturbance (Jonsen and Fahrig, 1997; Nordén et al., 2013; Gibbs and Stanton, 2001; Conole and Kirkpatrick, 2011). In Chapter II, we attempted to find the minimal set of mechanisms required to generate such a pattern. Among the models that we considered, we found that abovementioned pattern appears when both competitive interactions and demographic stochasticity are included (Fig. 8b). Under these conditions, the same pattern was observed for both fecundity and establishment models (II).

Earlier theoretical studies have found a similar non-monotonic pattern of abundance in model assuming a competition-colonization trade-off (Tilman et al., 1994, 1997; Neuhäuser, 1998; Weiner and Xiao, 2012; Nagelkerke and Menken, 2013). In these models, inferior competitors benefit from habitat destruction because of the demise of the superior competitors. In our model, the generalists become more competitive as specialists are disproportionately harmed by habitat loss. The shift in competitive ability allows the generalists to dominate at landscapes of intermediate quality by outcompeting the specialists.

Caveats

We assumed an idealized community in the sense that the specialist species had equal niche widths, their niches were equally spaced in the resource space, and they competed against a single perfect generalist species. Such ideal communities do not exist in nature, as there is a continuum of strategies between generalists and specialists. To relax this assumption, we could have simulated e.g. com-
communities composed of species with random niche width. In the mean-field fecundity model, the results would have been the same as what we obtained for the idealized community. For the other models the results could have been different, as they would have depended on the overlap of the niches. We selected to use an idealized community to make the interpretation of the results as easy as possible.

A further assumption of Chapter II was that the dynamics of the resource units are independent of the dynamics of the species. The model was motivated by wood decaying fungi which obviously contribute to the decay rate of occupied dead woods. A more realistic model could thus have coupled resource mortality with the consumption rate of the species.

The list of deviations between model assumptions and reality is like a never ending story. As one more example, in Chapter II we used a truncated top-hat dispersal kernel, which may not be very realistic, but was convenient from the computational point of view. While the shape of the dispersal kernel can make a difference, we note that some of the results were similar for models with a top-hat dispersal kernel and models without space (II).

Back to reality: conservation in Madagascar

Corridors are popular tools for conservation although their efficiency in enhancing the persistence of populations and species in the habitats that they connect remain contentious. In Chapter III, we analyzed the importance of the large-scale corridor that links Ranomafana National Park and Andringitra National Park.

First, we investigated the quality of the corridor in comparison with the quality of the national parks. Forest cover analysis showed that although the corridor is narrow at certain parts (Fig. 5c, denoted by stars), the interior of the corridor is still composed of intact forest that is more than 1 km wide. Hilty et al. (2012) suggests that a width of one kilometer or more should be sufficient to facilitate movements of vertebrates. The good quality of the corridor was reflected in the species composition: we found that in the year 2000, there was no difference in the community composition inside the corridor compared to the two parks (III). We concluded that in 2000, the quality of the corridor and the parks were equal.

Unfortunately, the situation is changing rapidly and is becoming worse. Deforestation rate has been high in the corridor between the years 2000 and 2012, during which period more than 400 km$^2$ of forest have been cleared. At this rate, the corridor will be wiped out by 2090.

To assess the consequences of deforestation for generalist and specialist species, we ran a spatially realistic metapopulation model (III) using the observed and possible future scenarios of forest cover. In general, we found that the corridor is most important for species with passive mode of dispersal (see Fig. 9 and Section: Influences of niche width and life-history on population dynamics). Species with active mode of dispersal may do equally well in the parks with and without the corridor, implying that for these species the parks are large enough to maintain viable populations.

However, the above conclusions are based on several assumptions that may not hold in practice. First, we assumed that the quality of the parks remains unchanged during the period when the corridor deteriorates. However, in Madagascar some parks, including Ranomafana national park, are subject to anthropogenic pressures such as illegal mining, selective logging, illegal trade, and bush meat hunting (García and Goodman, 2003; Barrett et al., 2010; Jenkins et al., 2011; Schwitzer et al., 2014), and therefore the plant and animal communities are increasingly vulnerable. Second, our classification of forest into intact and degraded forests is a gross simplification, as it assumes e.g. that all intact forests are uniform in their habitat type. In reality, many species are specialized to some specific habitat types found only within a subset of the parks, increasing their risk of extinction. Even if the corridor did not influence equilib-
rium occupancy of active dispersers in our model, we showed that further destruction of the corridor will greatly reduce gene flow (III). Reduced gene flow can lead to loss of genetic diversity and inbreeding depression, which will further increase the risk of extinction.

Software packages such as RAMSAS © and Vortex (Lacy, 1993) are focused on population viability analyses. These models can be fitted to particular populations and species but they require a large amount of data that are not often available. In contrast, our aim was to arrive at general conclusions about the effects of large-scale habitat corridor, and thus we used a more general model in Chapter III. It would have been interesting to conduct more detailed analyses but because most studies have been conducted in the national parks, data from the corridor are unfortunately scarce. To further increase our knowledge about biodiversity outside the national parks, more large scale studies are needed, such as the one conducted by Goodman and Razafindratsita (2001).

Recent studies show only limited evidence for any negative effects of corridors on biodiversity maintenance (Haddad et al., 2014), contrary to what was previously thought (Simberloff et al., 1992). In Madagascar, the Ranomafana-Andringitra corridor has existed for millennia, and it is most unlikely that its protection would have any negative effects on the communities of plants and animals. To conclude, the corridor, apart from facilitating individual movements and gene flow, functions as a refuge against the adverse effects of large-scale environmental stochasticity, it provides additional habitat over a large area, and it contributes to the genetic diversity of many species.

5 Concluding remarks
The overall goal of this thesis is to understand the role of space and dispersal that shapes past, present and future diversity. I addressed the questions of species diversification, coexistence and persistence in spatially structured environments. I mainly used theoretical approach by developing mathematical and statistical models that capture several biological processes. The models are still gross simplifications of the real biological systems, and whether or not those simplifications will matter or not is a key question for all modeling studies.

Phylogenetic comparative methods
In Chapter I, we developed a new type of phylogenetic comparative method to infer rates of diversification and colonization for multiple regions. Using Approximate Bayesian Computation instead of the exact likelihood approach gives more flexibility in model construction, e.g. allowing diversification rates to be diversity-dependent. Unfortunately, all these extensions come with costs that prevented us from estimating all model parameters separately. The inference was only possible when either extinction or within-region speciation rate was fixed.

Nevertheless, the GR model allows us to compare diversification rate for multiple regions, which is an advantage compared to GeoSSE, which is limited to only two regions. We found heterogeneous rates of diversification in the radiation of *Nanos-Apotolamprus* in Madagascar. Diversification rates in the North are significantly higher than those in the East and West. Further, we inferred a low colonization among the regions, which is in fact lower than the within-region extinction rates. Ecological studies indeed show that Malagasy dung beetles have low dispersal ability and narrow ranges, probably due to intense competition for resources that prevents species from expanding their geographical ranges.

We do not know whether the failure to estimate all the parameters independently is due to the ABC or the absence of information in the dataset. More studies are needed to understand the full potential of the GR model and the use of ABC before any routine application to empirical data are possible. It has been shown recently that State-Speciation-Extinction models contain flaws that elevate high Type I error (Maddison and FitzJohn, 2015; Rabosky and Goldberg, 2015). For instance, SSE models, including our GR, do not account for pseudo-replication. As a consequence, the correlation between spatial heterogeneity and diversification rates, like we have found for Malagasy dung beetles, needs to be interpreted with caution. The results would be more robust if the same conclusion was obtained for different datasets. The phylogenies and the distribution of several taxa (e.g., lemurs, amphibians, reptiles, and butterflies) are available for Madagascar, and thus can be used to compare with our results on dung beetles.

Ecology and conservation
During the past decade, metacommunity paradigms have become popular in explaining community assembly (Leibold et al., 2004). The modeling approach we used in Chapter II is an example where all four metacommunity paradigms can be included in a single model framework. One can compare the effect of spatial and non-spatial models, the difference between
deterministic and stochastic models, and the effect of the niche width of species. The integrative approach thus helps to gain insight about the effect of dispersal (mass effect paradigm), the role of stochasticity (patch occupancy and neutral paradigm), and niche width (species sorting paradigm). The modular framework is a promising approach to understand the effect of different mechanisms on community dynamics. It creates an array of theoretical predictions that can be tested empirically, and thus facilitates feedback between theoretical and empirical studies.

In addition to integrating different processes in the study of communities, there is also a need to integrate knowledge across different disciplines. We found an example of long-term eco-evolutionary dynamics where colonization and the dynamics of species’ geographical ranges influence the evolutionary processes of speciation and extinction, thus linking ecological and evolutionary processes. Conservation biology and practical conservation have largely focused on individuals and populations, but understanding community-level processes can be essential for choosing appropriate action. For instance, models that predict shift in species’ distribution in response to climate change can be misleading if species’ interactions are important but ignored (Davis et al., 1998). Finally, there is growing interest in linking phylogenetics to community ecology and to conservation (Webb et al., 2002). For instance, Faith (1992) suggested that phylogenetic diversity is a better measure of diversity than species richness and should replace or be taken into account in reserve selection. In this thesis, I have attempted to place evolution, ecology, and conservation under one umbrella.

Theoretical studies are making good progress in improving our understanding of the mechanisms of species assembly and especially in revealing how communities respond to habitat loss and fragmentation. Chapter II and III suggested that specialist species and passive dispersers will be most vulnerable to habitat destruction. But in the real world, the biodiversity crisis is on its way. In Madagascar, deforestation in the corridor between two large national parks occurs at a high rate and the entire corridor is in danger of disappearing by 2090. Thus, in addition to theoretical studies, actions are needed. Ecological processes are inevitably linked with socio-economic processes. The increasing threat to biodiversity in Madagascar is not only habitat loss and fragmentation but also continuous political crisis. Increasing poverty and corruption are the root causes of biodiversity loss in Madagascar and need to be tackled so that protected areas are protected not only on paper. What is needed is multiple actors from scientists to decision makers joining forces for conservation.

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Box 3: Mechanisms of coexistence
The theoretical study of coexistence has been greatly influenced by two empirical studies. On the one hand, Gause (1934) noticed that two paramecia (ciliate) species could not coexist in the same culture. A first generalization of the result called Gause’s principle or competitive-exclusion principle states that the number of competitors cannot exceed the number of distinct resources. However, the modern formulation states that the number of coexisting species is determined by the number of limiting factors. On the other hand, several species of plankton are seemingly able to coexist on a very limited number of resource types (Hutchinson, 1961). This observation is called the paradox of the plankton since it violates the competitive-exclusion principle.

Theoretical definition of coexistence
Two species coexist when both can attain a positive stable equilibrium in the presence of each other. However, studying the stability of multiple equilibria can be difficult. Instead, researchers now consider a sufficient condition for coexistence to be the mutual invasibility criterion (Chesson and Ellner, 1989; Chesson, 2000b). Here, coexistence is determined by the ability of an invading species to increase when the resident is at its equilibrium.

Spatial coexistence
The ability of species to coexist varies with the spatial scale. There are three hierarchical levels: microsites, habitat patch (corresponding to local populations), and region (landscape) (Leibold et al., 2004). The smallest scale is the microsite that can be occupied by just a single individual. This is a helpful concept especially for plants and sessile animals. A habitat patch is a collection of microsites located close to each other, while a region, the largest scale, is a network of habitat patches. Coexistence may occur at the patch or the regional level, but by definition is impossible at the microsite scale. Coexistence at the patch level implies coexistence at the regional scale but the converse is not true.

Competitive exclusion occurs whenever one species, the competitively dominant species, outcompetes the others. Studying coexistence thus means exploring ways to avoid, reduce or change competitive dominance in space and time. The relative strengths of interspecific competition vs. intraspecific competition is fundamental in determining coexistence or the lack of it. If interspecific competition is weaker than intraspecific competition, then mutual invasibility criterion will be met because at low density each species experiences relatively weak competition with the other species and can thus grow. The Lotka-Volterra model, which includes separate parameters for intraspecific and interspecific competition, shows clearly how the basic mechanism works (Lotka, 1932; Volterra, 1928). However, the generality of the Lotka-Volterra model is also its weakness because the competition parameters (the mechanism of competition) do not have any biological interpretation, and because it does not include resource dynamics.

In theory, if there is no overlap in resource use, there is no interspecific competition but intraspecific competition may be strong. In such a case, coexistence is easily attained. As overlap in resource use increases, competition between the species increases. The maximum amount of resource use overlap that still allows coexistence is called the limiting similarity (MacArthur and Levins, 1967; Abrams, 1983).

Theoretical models of coexistence investigate the mechanisms that influence the strengths of intraspecific and interspecific competition. The mechanisms of coexistence is one of the most intensively studied topics in theoretical ecology. Two important reviews of the mechanisms of coexistence are Chesson (2000b) and Amarasekare et al. (2004). Here, I divide the mechanisms of coexistence into two classes.

The first class is focused on differences in resource consumption rates and therefore takes explicit into resource dynamics. First, when the number of resources and the number of consumers are equal, coexistence is possible when species consume most the resource that is limiting most their own growth (Tilman, 1982). Second, when the number of consumers species exceeds the number of resource types, additional limiting factors are required. For instance, species can coexist when they have different functional responses (Armstrong and McGehee, 1980; Chesson, 2000b,a). This means that the consumption rates can be a linear or a nonlinear function of resource densities and become saturated at different resource levels (Armstrong and McGehee, 1980).
Storage effect is a mechanism that allows individuals to store energy gained during favorable period to help persist during an unfavorable period. If two species grow best during different periods, then the storage effect may prevent the exclusion of the disadvantaged species during the unfavorable period (Chesson, 2000a,b).

Generalist and specialist species may coexist when the generalist species can take advantage of the resources unexploited by the set of specialist species (Wilson and Yoshimura, 1994; Abrams, 2006). Coexistence is more likely if there is temporal variation in resources density, and if specialist species have a saturating functional response (Wilson and Yoshimura, 1994; Abrams, 2006).

The second class of models is concerned with spatial mechanisms. Perhaps the best known mechanism of coexistence is based on a trade-off between competition and colonization (Levins and Culver, 1971; Hastings, 1980; Hanski, 1983; Tilman et al., 1994; Yu and Wilson, 2001; Levine and Rees, 2002; Kisdi and Geritz, 2003; Kneitel and Chase, 2004; Amarasekare et al., 2004). Here, a superior competitor has lower colonization ability. An inferior competitor but superior colonizer can colonize resources not yet used by the superior competitor. A similar mechanism allows a weedy and a competitively dominant species to coexist at different successional stages at levels of disturbance (Pacala and Rees, 1998; Bolker and Pacala, 1999). The two species coexist when the frequency of disturbances are intermediate.

Heteromypia was coined to define the spatial scale of competition (Murrell and Law, 2003). When species are spatially segregated without differences in their niches, spatial segregation and thus coexistence is possible when the spatial scale of interspecific competition is much shorter than that of intraspecific competition (Murrell and Law, 2003). When spatial segregation is due to differences in performance in different habitat types, regional coexistence is possible. In this case, sufficient immigration can allow local coexistence (Loreau and Mouquet, 1999; Mouquet and Loreau, 2002).

Neutral models predict a special mechanism of coexistence without any differences among the species (Caswell, 1976; Bell, 2000; Hubbell, 2001). Coexistence under neutral model is not stable, but the relative abundances of the species enter a random walk and hence time to exclusion can be very long in large areas. Neutral models can be used as a null hypothesis for other mechanisms (Rosindell et al., 2011; Leibold et al., 2004).

Recently, Leibold et al. (2004) classified different mechanisms of coexistence at both local and regional scales. Coexistence in metacommunities depends on the relative strengths of dispersal, local selection, and stochasticity. The four metacommunity paradigms — mass effect, patch-occupancy, species-sorting, and neutral model — represent a convenient framework to classify communities and to guide empirical studies on coexistence and community organization at different spatial scale.
Box 4: Markov chains and processes

Markov chains and Markov processes are two widely used mathematical frameworks for modeling stochastic dynamics through time. A key property of Markov chains and Markov processes is the lack of memory in the sense that “the future states of a system only depends on its present state but not on its past states”. For instance, if an animal is at a location $x_t$ at the present time $t$, the probabilities of its future locations at times $t+1, x_{t+1}$ only depend on $x_t$ and not on its past locations $x_{t-1}, x_{t-2}, ...$. In a mathematical language, a random variable $X^*$ is called Markov chain if

$$P(X_{t+1} = x_{t+1}|X_t = x_t, X_{t-1} = x_{t-1}, ..., X_1 = x_1, X_0 = x_0) = P(X_{t+1} = x_{t+1}|X_t = x_t)$$

If the number of possible outcomes (states) is finite (say $n$), one can write the transition probability as a $n \times n$ matrix $P$ where $p_{i,j}$ represents the probability of moving from state $i$ to state $j$ during one time step. Knowledge about the transition probability matrix suffices to simulate the dynamics of the system through time. For instance, the following algorithm simulates a one dimensional random walk in which the individual moves one step up or down at each time step.

1. Start the simulation at some position $x$ at time $t = 0$.
2. Draw a random number $\rho$ between 0 and 1.
3. If $\rho < 0.5$, move one step up to $x + 1$, if not move down to $x - 1$.
4. Go to 1 by replacing $x$ with the new position and $t$ by $t + 1$.

Figure 10a shows the realizations of 5 random walks based on the above algorithm.

A Markov process is a continuous-time analogue of the discrete-time Markov chain. While Markov chain is defined by transition probabilities, a Markov process is defined by transition rates $r_{i,j}$. The waiting time is the time that the system stays in one state before moving to another. The waiting time for state $i$ follows an exponential distribution with parameter $R_i = \sum_j r_{i,j}$. For instance, the following algorithm simulates a continuous-time random walk that moves up at a rate $r_{1,2} = 2$ and moves down at a rate $r_{2,1} = 2$.

1. Start the object at some position $x$ at time $t = 0$.
2. Draw the waiting time $\tau$ from an exponential distribution with parameter $\lambda = r_{1,2} + r_{2,1}$.
3. Draw a random number $\rho$ between 0 and 1.
4. If $\rho < \frac{r_{1,2}}{r_{1,2} + r_{2,1}}$ move one step up otherwise move one step down.
5. Go to 1 by replacing $x$ with the new position an $t$ by $t + \tau$.

Figure 10b shows the realizations of 5 random walks for continuous time.

* The random variable is denoted by $X$ and its realization by $x$. For instance the result of flipping a coin is random variable, which can have the realization $x = \text{head or tail}$. A random variable is associated with a probability distribution where $P(X = x)$ is the probability that $X$ takes the value $x$.

Figure 10: Discrete-time a) and continuous-time b) random walks in one dimensional space.
Box 5: Bayesian inference and Approximate Bayesian Computation

Often the best way for describing and summarizing data is to fit a statistical model to it. In general, parameterizing a model with data involves the first step of choosing a model structure and the second step of estimating the parameters of the model. For example, the underlying model in linear regression is a linear relationship between a response variable \( y \) and an explanatory variable \( x \), and the assumption that the residuals (deviation of the data point from the model prediction) are normally distributed. In the linear regression, the underlying model represents merely a correlation between the variables, but in other types of model the relationship between the variables can involve also causal component.

Bayesian inference is a likelihood-based statistical framework for fitting models to data. A central role is played by the Bayes formula,

\[
P(\theta|\text{data}) \propto P(\text{data}|\theta) \times P(\theta).
\]

Let me explain these terms with an example. Assume that one is interested in finding the probability \( \theta \) that tossing a coin yields a head, and thus that it yields a tail with probability \( 1 - \theta \). The probability density of the prior distribution \( P(\theta) \) gives the initial knowledge about \( \theta \). For sure, in the coin tossing example \( \theta \) must be a number between 0 and 1 but the actual value is not known. If there would be no prior information at all, one could assume that all values are equally probable, and thus set \( P(\theta) = 1 \) so that it corresponds to a uniform distribution. But if we assume that the coin is fair, one could instead assume that \( \theta \) should be close to 0.5. In that case, we could choose some prior distribution with mean 0.5 and small standard deviation, say 0.1.

Now, data are needed to estimate \( \theta \). Let us assume that the coin is tossed \( n \) times and head showed up \( m \) times. Coin tossing follows a binomial distribution, so that the probability of obtaining \( m \) heads after \( n \) tosses is

\[
P(\text{number of heads} = m) = \binom{n}{m} \theta^m (1 - \theta)^{n-m}.
\]

More generally, \( P(\text{data}|\theta) \) is the probability of observing the data for a given parameter \( \theta \). \( P(\text{data}|\theta) \) is also called likelihood function and often written \( L(\theta|\text{data}) \).

The term on the left hand side of equation (1), \( P(\theta|\text{data}) \), represents the updated knowledge about the parameter \( \theta \), given the result of the tossing. Because \( P(\theta) \) and \( P(\text{data}|\theta) \) are known, it is possible to calculate \( P(\theta|\text{data}) \) using the Bayes formula. \( P(\theta|\text{data}) \) is the probability density of the posterior distribution.

Now, imagine that equation (2) would not be known, so that the likelihood of the data and thus the posterior distribution could not be computed. Approximate Bayesian Computation (ABC) is a tool that makes statistical inference possible also in such a case. The core idea of ABC is to replace the calculation of the likelihood by comparing observed and simulated data. ABC is a brute force method that is based on simulating many replicate datasets with the value of \( \theta \) drawn from the prior distribution with density \( P(\theta) \). In essence, ABC works like a colander so that only values of \( \theta \) that give similar number of heads with observed data are retained. The distribution of the retained \( \theta \) values is an approximation of \( P(\theta|\text{data}) \) and called approximated posterior distribution.

Following the colander metaphor, the key challenge for ABC is to decide the size of the holes. In technical term, the size of the hole is called tolerance. If the tolerance is too large, the approximated posterior distribution might not be close enough to the true distribution. If the tolerance is too small, only few parameter values will be retained and thus a very large number of simulations will be needed to get representative sample of the posterior distribution.

In general, comparing observed and simulated datasets is not as simple as in the coin tossing example. This is because the data can be multidimensional (e.g., phylogenetic trees) so that it is not obvious in which way the comparison should be made. In general, ABC uses summary statistics that captures information about the data. The choice of summary statistics depends on the information that is sought in the data. In the coin tossing example, a natural summary statistic would simply be the number of heads. In the case of a phylogenetic tree, the summaries might include the number of tips in a tree, the number of sister species, and so on. It can be shown that if the summary statistics capture all the information in the data that would be relevant for computing the likelihood, and when the hole size of the colander is small enough, the approximated posterior distribution converges to the true posterior distribution.