Spatial Patterns and Impact of Habitat Change on the Vertebrate Diversity of North-Western South America

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Spatial Patterns and Impact of Habitat Change on the Vertebrate Diversity of North-Western South America

Ph.D Thesis

Diego Francisco CISNEROS HEREDIA

Supervised by Dr Mark Mulligan (King’s College London)
Acknowledgements

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Abstract

Over the past two centuries, humans have become a global force able to change natural ecosystems at rates previously unseen. Human-driven habitat change has been identified as the anthropogenic action having the most widespread, intense, and extensive impacts on biodiversity. However, there are grave gaps in our knowledge about geographic, temporal and taxonomic factors related with the impacts and trends of habitat change on biodiversity. The north-western region of South America is globally noteworthy for its unique and rich flora and fauna. Studies on the biological evolution and biogeography of South America have typically analysed highland and lowland regions separately. However, spatial biodiversity patterns are still little known, and have not been properly analysed to reflect the complexity and coherence of the region. The aim of this thesis is to improve knowledge on the spatial patterns of vertebrate diversity in the region, in order to provide information to evaluate impacts caused by habitat changes and to evaluate the efficiency of in-situ conservation initiatives to mitigate negative impacts. I generate evidence to understand the impacts caused by habitat changes on species richness, endemism and distribution of amphibians, reptiles and birds of north-western South America. As part of the results of this thesis, in Chapter 2, I present a coherent and robust definition of north-western South America, allowing the update and refinement of the boundaries and definitions of the region from a biogeographic standpoint. In Chapter 3, I produce an integrated and updated assessment of the species richness and distribution patterns of more than 3000 species of anuran amphibians, squamate reptiles and birds; including calculations and comparisons of species richness and endemism patterns for the most relevant supra-generic taxa of the studied tax and, an evaluation of the biogeographic regionalisation of the region based on the newly-generated data for the studied taxa through cladistics biogeographic methods. In Chapter 4, I review the literature regarding impacts of habitat change on amphibians, reptiles and birds of the tropical Andes, developing
a systematic review and evidence synthesis. In Chapter 5, I generate evidence to understand the impacts caused by habitat changes on species richness and endemism of north-western South America by using a multi-taxonomic approach, including data from amphibians and reptiles. This chapter analyses a complex array of species with heterogeneous ecological characteristics and conservation status. The analysis includes updated data on amphibian diversity and provides for the first time a comprehensive evaluation of reptiles of the region. With these outputs, I evaluated the potential of natural protected areas, as in-situ conservation strategies in the region, to mitigate impacts of habitat change at all levels (geographic, ecological and taxonomic). In Chapter 6, I analyse the importance of habitat change as a factor that facilitates the establishment of non-native species. This study is based on information about the current status, invasiveness and potential impact of all non-native amphibians, reptiles and birds that have been reported in the Galapagos Islands.
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Chapter 1  Rationale and aims
1.1 Rationale

The north-western region of South America (NWSA) includes a mixture of tropical Andean highlands and lowland landscapes. The region is globally noteworthy for its unique and rich flora and fauna, with all major biomes occurring—i.e., rainforests, woodlands, scrublands, grasslands, and deserts (Barthlott et al., 2005; Duellman, 1988; Gentry, 1982; Guedes et al., 2018; Humboldt and Bonpland, 1807; Jenkins et al., 2013; Josse et al., 2011; Jørgensen et al., 2011; Lomolino et al., 2016; Mutke et al., 2011; Myers et al., 2000; Ulloa et al., 2017). There are numerous ecological and historical drivers of biodiversity, which may potentially vary among taxonomic groups and geographic areas (Kier et al., 2009). The complex geologic history and current topography of the Andes as well as its influence over the surrounding lands is apparently one of the main promoters of the evolution of range-restricted species with small distributions areas (Arteaga et al., 2016; Duellman, 1988; Lynch and Duellman, 1997). However, available biodiversity data, at all levels, is less robust for NWSA than for temperate zones. The study of the spatial biodiversity patterns of most vertebrate groups in NWSA remains incomplete. A significant and continued investment is needed to establish and maintain systematic biodiversity monitoring programmes in this region to generate reliable information for a better understanding of the situation and to contribute to conservation strategies and actions.

Human-driven habitat change, including land use and land cover modifications, has decreased natural ecosystems of NWSA (Klein Goldewijk et al., 2011; Williams, 2003, 2000; FAO, 2016b). Over the past two centuries, humans have become a force in the region able to change natural ecosystems at rates previously unseen (Hassan et al., 2005; Secretariat CBD, 2006, 2010a, 2014). Ecuador and Colombia, the two main countries in NWSA, had net loss in forested areas and in agricultural areas (FAO, 2016a).
1.2 Aims

The aim of this dissertation is to improve knowledge on the spatial patterns of vertebrate diversity in NWSA, in order to provide information to evaluate impacts caused by habitat changes and to evaluate the efficiency of in-situ conservation initiatives to mitigate negative impacts. I generate evidence to understand the impacts caused by habitat changes on species richness, endemism and distribution of terrestrial vertebrate animals of the Northern Andes, using a multitaxonomic approach to produce cost-effective and rapid evaluations.

I analyse a complex array of species with heterogeneous ecological characteristics and conservation status. The analysis includes updated data on bird and amphibian diversity and provide for the first time a comprehensive evaluation of the reptiles of the Northern Andes. I use spatial techniques and geographical information systems to estimate species geographic ranges and extinction risk. I evaluate the impact of human-drive habitat changes on the conservation of the three groups of animals from across the tropical Andes. In particular, I analyse the differences between species in terms of their geographical distributions, biogeographic perspective, and taxonomic relations. With all these outputs, I study the potential of natural protected areas in the tropical Andes to mitigate the impacts of habitat change for the different studied species, at all the different levels (geographic, ecological and taxonomic).

1.3 Objectives

Achieving the aim of this research entails the following objectives:

- Generate a new definition and description of NWSA and its internal physiography, reflecting the complexity and coherence of the region as a robust unit for biogeographic analysis, without ignoring its heterogeneous configurations in
space, time and form.

- Compile a comprehensive database of observation locality-points and natural history of birds, reptile and amphibian species from the Northern Andes.

- Provide a set of multi-taxonomic analyses to reveal region-wide patterns of the biodiversity composition of amphibians, reptiles and birds of NWSA in order to describe and compare their spatial patterns.

- Conduct a systematic review of the literature regarding impacts of habitat change on amphibians, reptiles and birds of the tropical Andes and to develop an evidence synthesis of the identified data

- Improve knowledge on the impacts caused by human-driven habitat changes on the biological diversity and to evaluate the efficiency of in-situ conservation initiatives to mitigate negative impacts.

- Analyse how habitat change may work as mediators of range expansion in species and as a factor that facilitates the establishment of non-native species.

1.4 Overview of thesis

This thesis contains five main chapters. An overview of what can be found in each chapter is given below:

CHAPTER 2: Review of physical geography and biogeographic regionalisation of north-western South America

The objective of this chapter is to generate a new definition and description of NWSA and its internal physiography, reflecting the complexity and coherence of the region as a robust unit for biogeographic analysis, without ignoring its heterogeneous configurations in space, time and form. This definition and
description of NWSA will be obtained through a narrative review and synthesis of the basic geologic and physiographic features that characterise north-western South America, which will allow the update and refinement of the boundaries and definitions of NWSA from a biogeographic standpoint.

CHAPTER 3: Spatial patterns of biodiversity and biogeographic regionalisation of amphibians, reptiles and birds in north-western South America

The aim of the present chapter is to provide a set of multi-taxonomic analyses to reveal region-wide patterns of the biodiversity composition of amphibians, reptiles and birds of NWSA in order to describe and compare their spatial patterns. These data will provide a more complete baseline for the biogeographic regionalisation of NWSA. I base this part of my investigation on a novel database generated for this study that combines a comprehensive, manually compiled distribution dataset for the three study groups. These analyses include: (i) an integrated and updated assessment of the species richness and distribution patterns of more than 3000 species of anuran amphibians, squamate reptiles and birds; (ii) calculation and comparison of species richness and endemism patterns for the most relevant supra-generic taxa of the studied tax and; (iii) evaluation of the biogeographic regionalisation of NWSA based on the newly-generated data for the studied taxa through cladistics biogeographic methods.

CHAPTER 4: Systematic literature review and evidence synthesis of impacts of habitat change on amphibians, reptiles and birds of the tropical Andes

It presents a systematic review of the literature regarding impacts of habitat change on amphibians, reptiles and birds of the tropical Andes and an evidence synthesis of the identified data.
CHAPTER 5: Impacts of human-driven habitat change on amphibians and reptiles of north-western South America

The aim of this research is to improve knowledge on the impacts caused by human-driven habitat changes on the biological diversity and to evaluate the efficiency of in-situ conservation initiatives to mitigate negative impacts. I generated evidence to understand the impacts caused by habitat changes on species richness and endemism of north-western South America by using a multi-taxonomic approach, including data from amphibians and reptiles. I analysed a complex array of species with heterogeneous ecological characteristics and conservation status. The analysis includes updated data on amphibian diversity and provides for the first time a comprehensive evaluation of reptiles of the region. With these outputs, I evaluated the potential of natural protected areas, as in-situ conservation strategies in the region, to mitigate impacts of habitat change at all levels (geographic, ecological and taxonomic).

CHAPTER 6: Habitat changes as mediators of natural colonisations and invasions by amphibians, reptiles and birds: Study case of the Galapagos Islands

I analyse the importance of habitat change as a factor that facilitates the establishment of non-native species. This study is based on information about the current status, invasiveness and potential impact of all non-native amphibians, reptiles and birds that have been reported in the Galapagos Islands.
References


Chapter 2  Review of physical geography and biogeographic regionalisation of north-western South America
2.1 Introduction

South America is one of the largest mainland masses in the world, with almost 8000 km from north to south and 18 million km² in surface. The general architecture, relief, climate, and landscapes have been largely shaped by tectonic forcing produced by extensive orogenic events occurring since the Neogene (Gregory-Wodzicki, 2000; Orme, 2015b; Rull, 2011). South America has three disjoint highland regions (the Andes, Guiana Shield, and Brazilian Shield), declining gradually in elevation until they get into a series of surrounding lowland basins (Orinoco, Amazon and Chaco-Paraná basins). While there are no clear-cut physiographic boundaries between them, all these regions are characterised by distinctive landscapes. Tropical lowlands¹ are the most extended landscapes in South America, while tropical highlands are mainly present across the Andes. Temperate landscapes are concentrated on the Southern Cone (Dunne and Mertes, 2015; Nores, 2004; Orme, 2015a; Spikings et al., 2015; Terán, 1984; Veblen et al., 2015; Winckell et al., 1997).

The north-western region of South America (NWSA) includes a mixture of tropical Andean highlands and lowland landscapes. The region is globally noteworthy for its unique and rich flora and fauna, with all major biomes occurring—i.e., rainforests, woodlands, scrublands, grasslands, and deserts (Barthlott et al., 2005; Duellman, 1988; Gentry, 1982; Guedes et al., 2018; Humboldt and Bonpland, 1807; Jenkins et al., 2013; Josse et al., 2011; Jørgensen et al., 2011; Lomolino et al., 2016; Mutke et al., 2011; Myers et al., 2000; Ulloa et al., 2017). Biodiversity of north-western South America has been shaped by major geological events, including closure of the Central American Seaway.

¹ Lowland areas in South America are usually below 1000 m, however, to establish a borderline would be arbitrary. The boundary between highland and lowland areas is better represented by a dynamic altitudinal band. The position and extension of such band depends of regional, local and temporal factors influenced by geology, physiography, biogeography, and human geography.
and formation of the Panama Isthmus, uplift of the Andes, geological marine transgressions, and Pleistocene climatic oscillations (Antonelli, Nylander, et al., 2009; Bacon et al., 2016; Duque-Caro, 1990; Frutos, 1990; Gentry, 1982; Haffer, 1970; Hooghiemstra and Hammen, 2004; Hoorn et al., 2010, 1995; Kroonenberg et al., 1990; Montes et al., 2015; Nores, 2004; Orme, 2015a; Quintero and Perktaş, 2018; Ramos, 2009).

Studies on the biological evolution and biogeography of South America have typically analysed highland and lowland regions separately (e.g., Dixon, 1979; Haffer, 1979; Lynch, 1979; Simpson, 1979; Vuilleumier, 1969, 1970; Vuilleumier and Monasterio, 1986; Weir, 2009). However, geologic and physiographic events act synergistically across South America, thereby promoting interacting changes in biodiversity across highlands and lowlands, and causing vicariance and dispersion events (Antonelli, Nylander, et al., 2009; Antonelli, Quijada-Mascareñas, et al., 2009; Brumfield and Edwards, 2007; Castroviejo-Fisher et al., 2014; Hoorn et al., 2010; Meserve, 2015; Orme, 2015a, 2015b; Parada et al., 2015; Rull, 2011; Weir and Price, 2011; Young, 2011; Young et al., 2015, 2002). Spatial biodiversity patterns are consequently more appropriately understood using regions defined upon an understanding of their space–time–form interactions (Knapp, 2005).

The biogeographic regionalisation of South America has a complex history, with many worldwide, regional or national frameworks proposed over the last 200 years (see Morrone, 2014a, 2017 for a detailed history of biogeographic regionalisation of South America). However, these proposals were, in most cases, hardly ever compatible and comparable in terms of methodologies, definitions, and boundaries; and some even proposed regions which were not natural areas (Morrone, 2014b, 2017). While Morrone (2014a,
2017) presents the latest biogeographical regionalisation proposal for the Neotropical region at the continental level, the spatial resolution is inadequately coarse for regional and local biogeographic analysis.

Despite extensive knowledge about NWSA, different sources have referred to this region indistinctly and without a proper definition. The objective of this chapter is to generate a new definition and description of NWSA and its internal physiography, reflecting the complexity and coherence of the region as a robust unit for biogeographic analysis, without ignoring its heterogeneous configurations in space, time and form. This definition and description of NWSA will be obtained through a narrative review and synthesis of the basic geologic and physiographic features that characterise north-western South America, which will allow the update and refinement of the boundaries and definitions of NWSA from a biogeographic standpoint proposed by Morrone (2014a, 2017).

2.2 Methodology

To produce a consistent area definition of NWSA, a literature review was conducted, focused on the basic features of the geology and physical geography of NWSA. The literature search was carried out during October 2017. Data sources included the library systems of The Maughan Library, King’s College London (London, UK) and the Biblioteca USFQ, Universidad San Francisco de Quito (Quito, Ecuador), Google Scholar™ scholarly texts search (https://scholar.google.com), and Google Books digital library (https://books.google.com). Keywords used for the database queries were: geolog*, geograph*, “South America”, “northern South America”, Andes,

2 Morrone’s map was converted into a polygon shapefile by Löwenberg-Neto (Löwenberg-Neto, 2014), but its scale and boundaries were not adjusted, just georeferenced.

3 “Literature review” is used according to the typology and definition of reviews presented by Grant and Booth (2009).
“Northern Andes”, Amazon*, “western Amazon”, Neotropic*, Pacific, Caribbean, Llanos, Orinoco, Magdalena, Ecuador, Colombia, in different combinations. Quotes represent queried expressions and asterisks represent any letter(s) following the keyword in the query. Phrasing was adapted to the requirements of each source database, together with the use of Boolean expressions.

To be eligible, citations must fulfil all criteria of a defined set. These criteria included: (i) research presenting geologic or physiographic information of South America; (ii) research focused on the Neogene and Quaternary geologic periods; (iii) primary and secondary sources. In addition to these criteria, the review focused on literature investigating at continental/subcontinental (America or South America), regional (i.e., northern, north-western, or western South America) or national (Colombia and Ecuador) scales. Studies at lower geographic scales were discarded if title-abstract screening revealed that its geographic scale was local only. Literature in Spanish, Portuguese or English was included. Conference abstracts, proceedings from conferences, and grey literature were excluded. In addition, potentially relevant records were identified by reviewing reference lists within identified papers already (Horsley et al., 2011). I screened titles and abstracts obtained from searches and retrieved full-text PDFs or printed documents of publications identified as potentially relevant. These citations were reviewed in full according to the same set of criteria. Publications eventually selected are those presented in this review. All relevant data was synthesised narratively, and scientifically established knowledge was cited using the most recent comprehensive literature.

To produce a refined version of Morrone’s proposal, I reviewed each biogeographic province according to the physiographic review, and adjusted the map by using the best available physiographic information at regional, national, and local scales, including the official geographic institutions of
Colombia (IGAC, 2016), Ecuador (IGM, 2017) and other regional geographic definitions (Cracraft, 1985; Duellman, 1988; Frutos, 1990; Gómez Tapia et al., 2015; Haffer, 1985; IDEAM et al., 2007; Josse et al., 2011; Porzecanski and Cracraft, 2005; Ramos, 2009; Sierra M., 1999; Terán, 1984; Vera, 2013; Vuilleumier and Monasterio, 1986; Winckell et al., 1997; Young, 2011), to an optimal resolution of 1 km².

2.3 Results

North-western South America (NWSA), as herein defined, includes the Northern Andes and all adjacent lowland environments. In the following paragraphs I provide an extensive review and synthesis of the geological and physiographic features of NWSA. For analytical reasons, subsequent sections will sector NWSA into the following regions:

- High Andean NWSA
- Trans-Andean NWSA
- Cis-Andean NWSA

2.3.1 High Andean NWSA

The Andes are the longest continental mountain range in the world, and the highest mountain range in the Western Hemisphere. The South American cordillera spans over 7000 km along the western part of subcontinent in length and about 300 km in width —except at its greatest width in the Bolivian flexure where its width expands to 640 km. The cordillera presents with an average height of about 4000 m, with the Aconcagua being its highest peak at 6961 m, and the summit of Chimborazo being the most distant point on the planet surface from the Earth’s centre with 6310 m from sea surface (Frutos, 1990; Gregory-Wodzicki, 2000; Orme, 2015b; Ramos, 1999). The Andes are widely recognised as one of the major geomorphological provinces of South America (Orme, 2015a). It is separated by the other two highland provinces (Guiana Highlands and Brazilian Highlands) by extensive lowland provinces
far from being a single geological unit, Andean geology has been produced by a great variety of processes, including plate subduction, magmatism, crustal shortening, terrain accretion, and isostatic adjustments (Orme, 2015a, 2015b, Ramos, 2009, 1999). Andean orogeny developed by subduction of oceanic crust along the continental margin. Subduction began in Late Proterozoic times, but the first phases of Andean orogeny are traced from the Jurassic. Significant uplifting started from the Cretaceous, and Andean main uplift began in the Miocene (Orme, 2015b; Ramos, 2009). Since tectonism, climate, and biomes are closely linked (Orme, 2015a), the Andes are a major biogeographic feature in South America. Uplift of the Andes had significant impacts on the distribution of biodiversity by imposing geographic barriers and elevation constraints, as well as by generating greater topographic complexity, resulting in large levels of biotic speciation and endemicity (Orme, 2015a).

Different areas of the Andes underwent unique development and show complex geological histories. Geological heterogeneity of the Andes has produced distinctive segments of asynchronous uplift and origin, while having in common geological and tectonic processes (Cediel et al., 2003; Gregory-Wodzicki, 2000; Kendrick et al., 2003; MéGard, 1987; Orme, 2015b; Ramos, 2009, 1999). Recognise consensus among authors exist on the existence of three major geological segments of the Andes, with distinctive magmatism and structural evolution and separated by flat-slabs with volcanic gaps: Northern, Central and Southern Andes (Gansser, 1973; MéGard, 1987; Orme, 2015b; Ramos, 2009, 1999). The Northern Andes have been recognised as a consistent domain of the Andes, based on their physical geography and geology (Cediel et al., 2003; Frutos, 1990; Jaillard et al., 2009; Kendrick et al., 2003; MéGard, 1987; Ramos, 2009). The Northern Andes coincide in their geological and geographic definition with the boundaries used herein for NWSA, which include parts of the following tectonic provinces: Andean
Orogenic Belt (including western lowlands and Andean highlands), Apure Basin, Llanos Basin, Oriente Basin, Guiana Shield, (which the extreme reaches Colombia, i.e., Chiribiquete), and Marañon Basin (which the extreme reaches extreme southern Ecuador and extreme northern Peru, i.e., Zumba and northern Huancabamba region) (Orme, 2015b).

The Northern Andes are the foremost physiographic feature in NWSA. The northernmost limit of the High Andes of NWSA is the Caribbean plate, and its northernmost portions are the Cordillera de Merida, a mountain range on the Maracaibo block that is separated from other Andean highlands by the Tachira Depression, and the Serranía del Perijá, a mountain range that extends into the Guajira Peninsula4 (Orme, 2015b; Ramos, 2009, 1999). The southernmost limit of the Northern Andes is usually established at the Huancabamba Depression5, which creates an east-west pass that interrupts the Andes and coincides with the southern extremes of the Gulf of Guayaquil and the Amotape-Tauhin terranes (Cediel et al., 2003; Mourier et al., 1988; MéGard, 1987; Ramos, 2009; Weigend, 2002).

The High Andes of NWSA are agreeingly divided into distinct mountain ranges across Colombia and Ecuador. In Colombia, three mountain ranges are differentiated:

(i) The Cordillera Oriental is the easternmost mountain range of the Andes in Colombia, extending for 1200 km from the Serranía del Perijá to the Serranía de La Fragua; the latter connects with the Macizo Colombiano (Colombian Massif) or Nudo de Almaguer in the

4 While Caribbean mountain ranges on northern Venezuela are related to Andean orogeny — i.e., Cordillera de la Costa and Serranía del Interior, their tectonic elements were produced by different geological processes (e.g., metamorphism) and are thus not included in most definitions of the Northern Andes (Orme, 2015b; Ramos, 2009, 1999).

5 The geological name of this structural zone is Huancabamba Deflection (Ramos, 2009).
Cordillera Central. It is composed of a Precambrian and Paleozoic basement deformed by pre-Mesozoic orogenic events.

(ii) The Cordillera Central is the shortest (about 1000 km), and the most volcanic of the three Andean mountain ranges of Colombia. It extends from the Serranía de San Lucas to the Nudo de los Pastos—the latter connects with the Cordillera Occidental. At its southern end, lies the origin of the four most important rivers of Colombia: Magdalena, Cauca, Patía and Caquetá. The Cordillera Central is composed of a pre-Mesozoic basement, including oceanic and continental rocks, intruded by Mesozoic and Cenozoic plutons related to subduction.

(iii) The Cordillera Occidental is the westernmost and narrowest of the three mountain ranges of Colombia. It extends across 1200 km, from the Nudo de Paramillo to the Nudo de los Pastos. At the Nudo de Paramillo, the Cordillera Occidental splits into three parallel branches: Serrabía de Abibe, Serranía de San Jerónimo, and Serranía de Ayapel. The Nudo de los Pastos or Macizo de Huaca is a large mountain massif and one of the most important orographic features of the High Andes of NWSQ. It is composed of oceanic rocks accreted during the Mesozoic and early Cenozoic.

The Cordillera Occidental and Cordillera Central of Colombia and are separated by the depressions of the Cauca and Patía rivers. These mountain ranges run almost parallel to the Pacific coast, joining only twice—at the Marmato and Tambo mountain bridges. The Cordillera Oriental separates from the Cordillera Central from the Colombian Massif in direction NE, and are separated by the River Magdalena Valley. The River Magdalena Valley is one of the most characteristic and geologically complex areas on the north of the Andes. The middle and upper part of the Magdalena Valley are Neogene fluvial depositions controlled entirely by volcanism of the surrounding mountain ranges, while the lower part is an
Oligocene to recent forearc basin associated with subduction, and part of Trans-Andean NWSA (Bernal, 2016; Cooper et al., 1995; Hoorn et al., 1995; IGAC, 2016, 2005, 2002; Mora-Bohórquez et al., 2017; Nie et al., 2010; Ramos, 2009; Taboada et al., 2000; Vera, 2013).

To the south of the *Nudo de los Pastos*, the Andes get into Ecuador divided into two mountain ranges:

(i) The **Cordillera Occidental** is the westernmost mountain range of the Andes in Colombia. It extends across 500 km, from the Nudo de los Pastos south to the *Macizo del Cajas* (Cajas Massif). Its western slope is continuous with the western slope of its homonym mountain range in Colombia. It is composed of oceanic rocks accreted during late Cretaceous and early Tertiary. The Chimborazo volcano (6310 m elevation) and the Cotopaxi volcano (5900 m elevation) are part of Cordillera Occidental and are the highest peaks along the Equatorial line.

(ii) The **Cordillera Real** (also called **Cordillera Oriental**), which, despite its name, is a continuation of the Cordillera Central of Colombia, extends from the Nudo de los Pastos to the *Contrafuerte de Lagunillas*, and reaches into Peru along low mountain ranges that reach the Huancabamba Depression. It is a metamorphic belt that over thruts the sub-Andean zone located eastward, along the North Andean Frontal fault.

Towards the south of the Cajas Massif, where the Cordillera Occidental ends, several west-east oriented mountain ridges appear, with neither a dominant central valley nor Holocene to recent volcanism, and a very different geological configuration to that of the northern mountain ranges (Acosta Arteaga, 1976; Bernal, 2016; Cediel et al., 2003; Coltorti and Ollier, 2000; Hall and Wood, 1985; Hughes and Pilatasig, 2002; IGAC, 2016, 2005, 2002, IGM, 2009, 2012, 2000; Kroonenberg et al., 1990; A. Lavenu et al., 1995; Lips, 1998;
Pennington, 1981; Ramos, 2009; Restrepo et al., 1985; Tamay et al., 2016; Terán, 1984; Veblen et al., 2015).

The two Ecuadorian mountain ranges are separated on the north by the Inter-Andean Depression, but volcanic mountain bridges (locally called nu dos) form escalated interruptions, leaving sedimentary intermontane basins in between. The Inter-Andean Depression is an intervening structural depression, 20-40 km wide, 300 km long, and occurring at 2000-3000 m elevation, filled with volcanic deposits related to stratum volcanoes. The origin and shape of the Inter-Andean Depression are attributed to complex faulting. Due to the high elevation of these areas, mountain bridges only provide biogeographic joints for highland biodiversity. On the south, the configuration of the Andes is different—Cordillera Occidental ends at the Cajas Massif, and Neogene-Quaternary basins of Azogues-Cuenca-Nabón, Loja, Malacatos-Vilcabamba, while Catamayo extends between the Cordillera Oriental and the low southern mountain ranges that constitute the western Andes of Ecuador. These southern basin are filled with Miocene to Quaternary sediments, and have Cretaceous detrital (Alain Lavenu et al., 1995; Alvarado et al., 2014; Barragán et al., 1996; Coltorti and Ollier, 2000; Ego and Sebrier, 1996; IGM, 2009, 2012; Lips, 1998; Marocco, 1994; Marocco et al., 1995, 1995; Ramos, 2009; Tamay et al., 2016; Terán, 1984; Vera, 2013).

The Sierra Nevada de Santa Marta is a triangular-shaped mountain range near the Caribbean coast. It covers about 17000 km² and contains the highest peaks in Colombia (up to 5775 m elevation). Sierra Nevada is separated from the Andes by the River Cesar Depression, and although it is associated with Andean orogeny, it constitutes a separate geological, geographic and biotic unit (Bernal, 2016; Chapman et al., 1917; IGAC, 2016; Macdonald and Hurley, 1969; Tschanz et al., 1974).
In Ecuador, smaller mountain ranges, usually geologically older than the Andes, were produce before and along Andean orogeny on the eastern side of the Andes. They are part of the Sub-Andean zone and include two uplifts, separated from each other by the Pastaza Depression: the Napo Antiform (with the Cordillera de los Guacamayos-Sumaco-Galeras) and the Cutucu Antiform (Cordillera del Kutuku and Cordillera del Cóndor). These uplifts are composed of Jurassic-Neogene sedimentary formations and Triassic volcanic rocks. Although these mountain ranges are distant from the Andes, they are not completely separated by lowland areas, and show abiotic and biotic similarities and associations with the Andes. They are thus considered part of the High Andes of NWSA (Bernal, 2016; Bès de Berc et al., 2005; Coltorti and Ollier, 2000; IGAC, 2016; IGM, 2012; Roddaz et al., 2012; Terán, 1984).

2.3.2 Trans-Andean NWSA

Trans-Andean NWSA includes lowlands on the Pacific and Caribbean sides of the Andes. The northernmost limits of Trans-Andean NWSA are Humboldt Bay, Serranía del Darién, the Gulf of Urabá, the Caribbean coast, the Peninsula de la Guajira, and the Maracaibo Basin, inclusively. The southernmost limits are the Gulf of Guayaquil, Tumbes Bay—a few kilometres to the south of the border between Ecuador and Peru, and the Amotape-Tauhin terranes (Arnaiz-Rodríguez and Audemard, 2014; Bernal, 2016; Chapman, 1926; Chapman et al., 1917; Cracraft, 1985; Duellman, 1979, 1999; Duque-Caro, 1990; Haffer, 1970; Mourier et al., 1988; Ramos, 2009; Veblen et al., 2015; Weigend, 2002). Trans-

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6 Three mountain ranges on the Pacific lowlands of Colombia and Ecuador (i.e., Serranía del Darién, Serranía del Baudó, and Cordillera de la Costa), and one mountain range on the Caribbean lowlands of Colombia (Serranía de Macuira) are disconnected and isolated from the Andes, have different geological origins, and are treated as part of Trans-Andean NWSA. Two mountain ranges on the Amazonian lowlands of Colombia (i.e., Serranía de la Macara and Serranía de Chiribiquete) are not related to the Andes as they are part of the Guiana Shield, and are considered as part of Cis-Andean NWSA.

7 See footnote 1.
Andean NWSA extends across 1500 km along the Pacific continental margin and across 600 km alongside the Caribbean margin. The Pacific lowlands are about 60–100 km wide across—except at its greatest width in the Gulf of Guayaquil where they are 230 km wide. The Caribbean lowlands are much wider along the River Magdalena basin, but remain surrounded by mountain ranges towards La Guajira (IGAC, 2002, 2016; IGM, 2012; Terán, 1984).

The coastline of NWSA was produced by complex and asynchronic convergence of the Cocos, Nazca and Caribbean oceanic plates with the South American continental plate (Hall et al., 2008; Jaillard et al., 2009; Marcaillou et al., 2016; Orme, 2015a, 2015b; Pennington, 1981; Taboada et al., 2000). Closure of the Central American Seaway and formation of the Panama Isthmus, and uplift of the Andes are the most geologically significant tectonic events that shaped the lowlands of Trans-Andean NWSA (Coates et al., 2004; Duque-Caro, 1990; Ibaraki, 1997; Jackson et al., 1996; Jaillard et al., 2009; Leigh et al., 2014; Montes et al., 2015; Veblen et al., 2015). The Caribbean plate and accreted volcanic terranes of western Colombia and Ecuador formed during the Cretaceous; the Caribbean plate subsequently migrated to the northeast. The interactions with the Panama microplate and the Central American volcanic arc eventually led to the creation of the Central American Isthmus. The Darien region of Panama and the River Atrato basin of Colombia are the easternmost part of the isthmus (Coates et al., 2004; Farris et al., 2011; Ibaraki, 1997; Jackson et al., 1996; Jaillard et al., 2009; Kerr and Tarney, 2005; Leigh et al., 2014; Orme, 2015b, 2015a). Subduction of oceanic terraces beneath the South American plate during Mesozoic and Cenozoic Andean orogeny produced the closure of the trans-Andean seaways in Ecuador, and the accretion of oceanic terranes that formed the Pacific lowlands and the Cordillera Occidental of Colombia and Ecuador (Coltorti and Ollier, 2000; Hall et al., 2008; Hughes and Pilatasig, 2002; Jaillard et al., 2009; Kennan and Pindell, 2009; Kerr et al., 2002; Marcaillou et al., 2016; Mourier et al., 1988; Orme, 2015a, 2015a; Pennington, 1981; Reynaud et al., 1999; Taboada et al., 2000). Tectonically, the Pacific
coastline corresponds to the Northern Andean margin, and the southern border of NWSA is closer to the Carnegie Ridge (Cediel et al., 2003; Gutscher et al., 1999; Hall et al., 2008; Kellogg and Mohriak, 2001; Reynaud et al., 1999; Veblen et al., 2015).

The Pacific lowlands of NWSA extend over 180000 km², across the western lowlands of Colombia, Ecuador and extreme northern Peru. The orography of the Pacific lowlands is fairly uniform, except for the presence of the Serranía del Darién and Serranía de Baudó in Colombia and the Cordillera de la Costa in Ecuador, which are low volcanic mountain ranges that run just inland from the coastline and almost parallel to the Andes (Bernal, 2016; Cediel et al., 2003; IGAC, 2016, 2005; IGM, 2012; Restrepo et al., 1985; Terán, 1984). Serranía del Darién, which marks the border between Colombia and Panama, is about 260 km long, about 500 m high on average, and reaches its highest elevation (1690 m) at the Alto de Nique. Serranía del Baudó runs from extreme south-eastern Panama to Cabo Corrientes in northwestern Colombia. It is about 235 km long and reaches 1030 m in altitude at Alto del Buey. Cordillera de la Costa is a broad terminology applied in Ecuador to a group of several small mountain ranges crossing for about 350 km, reaching elevations mostly between 400 and 600 m. The highest elevations are located in the Cordillera de las Delicias at about 850 m: Montañas de Viche, Montañas de Mache, Montañas de Chindul, Montañas de Jama-Pedernales, Cerros de Jipijapa, Cordillera de Delicias, Cordillera Chongón-Colonche (IGM, 2012, 2009; Restrepo et al., 1985; Terán, 1984; Winckell and Zebrowski, 1997).

There are eight main rivers that run across the Pacific lowlands of NWSA: Atrato, Baudó, San Juan, Patía (in Colombia), Santiago-Cayapas, Esmeraldas, Guayas, and Tumbes-Puyango (in Ecuador). Due to tectonic uplifting of the Andes, these rivers—except for the Atrato, drain into the Pacific Ocean. The River Atrato Basin—the largest river in the Pacific lowlands of Colombia,
empties into the Gulf of Urabá (Bernal, 2016). Most rivers draining into the Pacific and Caribbean slopes are usually short and steep. The Guayas river has a lengthier runout across a broad sedimentary basin. The River Guayas, and its tributaries, form the largest estuary on the Pacific coast of South America, and are referred to as the Gulf of Guayaquil (drainage based area ca. 33000 km²) (Terán, 1984; Twilley et al., 2001).

The Caribbean lowlands of NWSA extend over 130000 km² on the north of Colombia, from the Serranía del Darién and the Gulf of Urabá to the Serranía de Perijá and the Gulf of Venezuela, including the Península de la Guajira. The orography of the Caribbean lowlands is uniform except for the Sierra Nevada de Santa Marta, which extends to the north, and the Serranía de Macuira at the La Guajira Peninsula—a small mountain range of 35 km long and with its highest peak reaching 864 m. The Caribbean lowlands include the Magdalena and Cauca river basins. The River Magdalena constitutes one of the most important hydrologic features of Colombia, modifying both highlands and lowlands (drainage basin 250000 km², total sediment load 220 million metric tons per year, and sediment yield 920 metric tons per km² per year; Milliman and Syvitski, 1992). The headwaters of River Magdalena are in the highlands between the Cordillera Central and Cordillera Oriental, and its mouth empties into the Caribbean Sea. Along its course, the Magdalena receives many tributaries, with the largest contributors being the Cauca, Cesar and San Jorge rivers, which join along the Caribbean lowlands. The headwaters of River Cauca are near the sources of the River Magdalena but the River Cauca runs north between the Cordillera Central and Cordillera Occidental of Colombia. The Cauca is the main tributary of the Magdalena, flowing into it at the

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8 Although the hydrographic association of the lowlands of western Colombia is usually referred to the Pacific Ocean, more than a third of them actually drain into the Caribbean Sea.

9 Sediment yield is calculated as the sediment load divided by basin area (Milliman and Syvitski, 1992).
Mompox Depression, in the Caribbean lowlands (Bernal, 2016; Chapman et al., 1917; IGAC, 2016, 2005).

2.3.3 Cis-Andean NWSA

Lowlands\(^1\) east of the Andes occupy the largest surface area in NWSA. Most of these vast lands are at elevations below 500 m, going down to 200 m in Amazonian Ecuador, and to 90 m in the Amazonia of extreme southern Colombia. Cis-Andean NWSA extends north to the Cordillera de la Costa, Serranía de Turimiquire, and surrounding massifs; and south to the Marañon and Amazonas rivers. West, Cis-Andean NWSA is bordered by the Cordillera Oriental of Colombia and the Cordillera Real of Ecuador, while east, the Guianan Shield and the Negro and Amazonas rivers form the boundaries of the region (Cooper et al., 1995; Cracraft, 1985, 1974; Dinerstein et al., 1995; Hoorn et al., 2010, 1995; Morrone, 2017; Olson et al., 2011; Roddaz et al., 2012).

The geological history of Cis-Andean NWSA was strongly influenced by the uplift of the Andes, more specifically the Cordillera Oriental and Cordillera Real during the Miocene and its relation with the Precambrian Amazonian craton. Cis-Andean NWSA is composed of several intracratonic basins that are separated from one another by structural arches that have deeply influenced the patterns of drainage and sedimentation of the entire region. During geological times, oceans reached the entire Orinoco basin and probably entered western Amazonian lowlands. The drainage of the Amazonas and Orinoco flowed northward until the middle Miocene, but diverted with the uplift of the Andes. The basins of the Amazonas and Orinoco became distinctly separated by the uplift of the Vaupes arch (Cooper et al., 1995; Hoorn et al., 1995; Hovikoski et al., 2009; Orme, 2015a, 2015b; Roddaz et al., 2012).

The most distinctive physiographic features of the Cis-Andean lowlands of NWSA are the large rivers flowing eastwards, most of them with headwaters
in the Andes and belonging to two main river basins: River Amazonas basin and River Orinoco basin. Most rivers in Cis-Andean NWSA drain from the eastern slopes and foothills of the Andes, initially descending steeply, and thereafter running across lengthy and broad sedimentary basins until eventually joining the basins of the two large rivers. River Amazonas basin drains around one-third of the continent, with a drainage basin of 6.1 million km\(^2\) (total sediment load 1200 million metric tons per year, and sediment yield 190 metric tons per km\(^2\) per year; Milliman and Syvitski, 1992), while the River Orinoco has a drainage basin 1.1 million km\(^2\) (total sediment load 150 million metric tons per year, and sediment yield 150 metric tons per km\(^2\) per year; Milliman and Syvitski, 1992; Orme, 2015a).

2.3.4 Climate and vegetation of NWSA

The emphasis of this review is not on climatic and vegetation features of NWSA. Only a general overview is presented herein. NWSA lies within tropical latitudes and has the direct influence of the Intertropical Convergence Zone. Climate in NWSA is usually moist, with low thermal seasonality, temperature variability driven by elevational gradients and air humidity, and significant diurnal temperature variations. The Pacific lowlands are mostly tropical wet across western Colombia and north-western Ecuador, and then gradually become drier. Climate of the region is directly influenced by the Pacific Ocean, although to a limited extent due to the rather narrow coastal strip. Tropical Pacific influences are aided by tropospheric subsidence, the Humboldt and El Niño currents. Seasonality is a main driver of these transformations, with general patterns showing: (i) tropical very wet zone\(^{10}\) with low seasonality (mean annual rainfall >3000 mm, 0 dry months); (ii)

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\(^{10}\) Typical tropical very wet localities are the River Cayapas basin (Ecuador) in Trans-Andean NWSA.
tropical very humid zone\textsuperscript{11} with slight seasonality (annual rainfall 2000–4000 mm, 0–4 dry months); (iii) tropical humid zone\textsuperscript{12} with mid seasonality (annual rainfall 600–2500 mm, 4–6 dry months); tropical semiarid zone\textsuperscript{13} with strong seasonality (annual rainfall 300–1500 mm, 6–11 dry months); and tropical arid zone\textsuperscript{14} with low seasonality (mean annual rainfall <400 mm, 11–12 dry months). The Amazonian lowlands fall mainly within the tropical humid, very humid and wet zones—with wet localities concentrated towards the foothills of the Andes, while the Orinoco lowlands are drier and more seasonal. Moist surface winds from the lowlands penetrate inland towards the High Andes, bringing clouds and rain to the slopes of the different mountain ranges. Biomes are closely linked to climate, and due to the large climate variation in NWSA, a shifting ecological mosaic is present. Tropical wet and very humid zones are covered by rainforests, tropical humid zones by seasonal semideciduous/dry forest, and tropical semiarid and arid zones by dry forest. Strong ecological elevational zonation is different between Andean slopes and intermontane valley flanks. Cloud forests are characteristic at elevations between 1900 and 2400 m, due to concentration of pluviometric optimum maxima. Upper highland areas have a characteristic vegetation of NWSA, the paramo grasslands, which extend from the upper tree line to the snow line at 4500 m (Bernal, 2016; Buytaert et al., 2006; Hoorn et al., 2010; IGAC, 2016, 2002; Martínez et al., 2011; Orme, 2015a; Poveda et al., 2006;

\textsuperscript{11} Typical tropical very humid localities are the River Baudo basin (Colombia) and the Upper Guayllabamba basin (Ecuador) in Trans-Andean NWSA.

\textsuperscript{12} Typical tropical humid localities are Zaruma (Ecuador) and Quininde (Ecuador).

\textsuperscript{13} Typical tropical semiarid localities are Bahía de Caraquez (Ecuador) and Barranquilla (Colombia).

\textsuperscript{14} Typical tropical arid localities include the Santa Elena Peninsula (Ecuador), La Guajira (Colombia), and Tumbes (Peru).
Terán, 1984; Veblen et al., 2015; Winckell, 1997; Winckell et al., 1997; Young et al., 2015).

2.4 Discussion

2.4.1 North-western South America is a coherent and robust unit

The geologic and geographic synthesis presented herein allows to recognise north-western South America (NWSA) as a distinct unit. It has common geologic, physiographic, climatic and biotic frameworks, but also important intra-heterogeneity (Albert et al., 2006; Brumfield and Capparella, 1996; Cediel et al., 2003; Duellman, 1979; Gentry, 1982; Mapes et al., 2003; Poveda et al., 2006; Spikings et al., 2015). NWSA shares geological and geographic features with surrounding areas, e.g., the Andes or the Amazonian lowlands, but there are clear demarked boundaries that not only allow to differentiate NWSA from other part of South America, but that may work as active or past biogeographic barriers. For example, the Tachira and Huancabamba depressions reach low elevations and are major physiographic and ecological barriers today—and during glacial times, for animal and plant communities (Cracraft, 1985; Duellman, 1999; Duellman and Wild, 1993; James and Sacks, 1999; Parker et al., 1985; Prado and Percequillo, 2017; Vuilleumier, 1969; Vuilleumier and Ewert, 1978; Weigend, 2002). On the other hand, the River Negro and the River Amazonas have been identified as important barriers to gene flow of several groups of vertebrates (Bouli et al., 2008; Naka et al., 2012; Ribas et al., 2012). The fundamental character of NWSA is, as well as for the entire continent, driven by tectonic forcing. Tectonism shapes positions and relieves, which influence and are modified by climate, and in turn affect biodiversity (Orme, 2015a). Biodiversity evolution does not solely depend on geology, geography and climate, but it is greatly impacted by them.
2.4.2 Biogeographic regionalisation of NWSA refined

Morrone’s regionalisation has several advantages over previous proposals. It is (i) evidence-based, using qualitative and quantitative biodiversity data; (ii) methodologically-sound, using cladistics principles applied to biogeography; (iii) unbiased by taxonomy, based on data from plants, invertebrates and vertebrates; and (iv) standardised, with nomenclature and definitions following the International Code of Area Nomenclature (Ebach et al., 2008). However, Morrone’s proposal scale is coarse? . When applied at regional levels, there are some inconsistencies between the area definitions and map boundaries. For some biogeographic areas, these inconsistencies have been revised and corrected (Arana et al., 2017; Morrone et al., 2017), but inaccuracies still remain uncorrected in north-western South America. Precise limits for biogeographic provinces are always difficult to establish at a very fine level, due to the existence of natural ecotones, distribution variation among species, anthropogenic habitat changes that obscure original ecological distribution, among others. However, more accurate boundaries, with explicit ranges to describe the associated uncertainty, are necessary for biogeographic analysis at regional and local levels. Based on the physiographic and geologic review, the following biogeographic regions are defined and adjusted accordingly (
Figure 1):

Sierra Nevada province Müller, 1973: This province is herein recognised and separated from the Guajira province based on its distinctive geologic, physiographic, and biotic features (see Chapter 3, Hernández-Camacho et al., 1992; Müller, 1973). It is defined to include the slopes and highlands of the Sierra Nevada de Santa Marta that rise from the Caribbean lowlands of northern Colombia.

Guajira province Cabrera & Willink, 1973: It is herein restricted to, and defined to include, the Caribbean lowlands of Trans-Andean NWSA, on northern Colombia and extreme north-western Venezuela, from the Serranía del Darién and the Gulf of Urabá to the Serranía de Perijá and the Gulf of Venezuela, including the Península de la Guajira, the Maracaibo Basin, but excluding the low River Magdalena valley.

Magdalena province Müller, 1973: It is herein redefined to include the low River Magdalena valley, up to 1000–1300 m elevation on the foothills of the Cordillera Central and Cordillera Oriental of Colombia, but excluding the upper and middle River Magdalena valley, which has closer geologic and physiographic associations with the Andes.

Chocó-Darién province Ryan, 1963: It is defined to include the lowlands and highlands of southeastern Panama and western Colombia (incl. Serranía del Darién, Serranía del Sapo, Altos de Nique, and Serrania de Baudo), and the Pacific lowlands and Andean foothills, below 1000–1300 m elevation, of western Colombia and northwestern Ecuador. Southern boundaries include the Esmeraldas and Guayllabamba rivers.
Western Ecuador province Dinerstein et al. 1995: It is defined to include the lowlands and foothills of western Ecuador (including the Cordillera de la Costa), below 1000 m elevation. On the north, boundaries are the Esmeraldas and Guayllabamba rivers, but towards the south the boundaries are not geographically apparent. The province in general is linked with the tropical humid climatic zone, and seems to be controlled by its seasonality and linked with rain shadow effect on the Cordillera de la Costa and western slopes of Cordillera Occidental of Ecuador (Anderson and Jarrín-V, 2002; Cisneros-Heredia, 2006, 2007; Dodson and Gentry, 1991).

Ecuadorian province Müller, 1973: As well as the Western Ecuador province, the borders of this region are not geographically apparent but climatically linked. The province in general is linked with the tropical semiarid and arid zones, and is controlled by the effect of the Humboldt oceanic current (Dodson and Gentry, 1991; Linares-Palomino et al., 2011; Pennington et al., 2000).

Sabana province Orfila, 1941: It is defined to be equivalent to the Llanos region of Venezuela and Colombia, its southern border herein being specific at the River Meta. The Sabana province was classified by (Morrone, 2014a) as part of the Pacific dominion, however, its geographic, geologic, and biotic association is with Cis-Andean NWSA (see Chapter 3).

Imerí province Beven et al., 1984: It is defined to include the Cis-Andean lowlands of NWSA between the River Meta on the north, and the upper Caquetá and lower Napo rivers on the south. To the east the boundaries are with the Negro and Amazonas rivers, and to the west with the foothills of Cordillera Oriental of Colombia, below 1000–1300 m elevation.

15 Morrone (2014a) cited Morrone (1999) as author of the name of this region, however, Dinerstein et al. (1995) were the first authors to identify and name this region, using the name “Western Ecuador Moist Forest ecoregion”.

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Napo province Müller, 1973: It is herein defined to include the Cis-Andean lowlands of NWSA between the upper Caquetá and lower Napo rivers on the north, and the River Marañon on the south. To the east, the boundary is at the joint between the Napo and Marañon rivers, and to the west is with the foothills of Cordillera Real of Ecuador, below 1000–1300 m elevation.

Yungas province Cabrera, 1971: This province only slightly gets into NWSA, through the Marañon valley that reaches extreme southern Ecuador and northern Peru, reaching slightly beyong the Huancabamba Depression. It is herein not revised due to its extralimital nature.

The High Andes are probably the most complex region in NWSA. Morrone (2014a, 2017) recognised two different biogeographic provinces: Cauca and Paramo provinces. However, geologic and geographic data points out to further biogeographic diversity to be recognised, at least separating different biogeographic regions in relationship to the configuration of the different mountain ranges. In the absence of further data, it is recommended that more biogeographic analyses should be conducted with further division within the High Andes in order to solve its biogeographic regionalisation and biotic relationships.
Figure 1. Biogeographic provinces of north-western South America
References


Chapter 3  Spatial patterns of biodiversity and biogeographic regionalisation of amphibians, reptiles and birds in north-western South America
3.1 Introduction

The central goals of biogeography are to study spatial patterns of biological diversity; understand the underlying abiotic and biotic factors that influence biological diversity across space, time and form; identify and organise Earth into natural biotic regions; and better grasp the consequences of global changes in order to prioritise in-situ biodiversity conservation actions (Ebach, 2015; Knapp, 2005; Lomolino et al., 2016; Morrone, 2009). To fulfil these goals, the spatial dimensions of biodiversity need to be well-understood and delimited.

North-western South America (NWSA) is celebrated for its megadiverse flora and fauna as well as its high proportion of endemic species (Barthlott et al., 2005; Duellman, 1988; Gentry, 1982; Guedes et al., 2018; Humboldt and Bonpland, 1807; Jenkins et al., 2013; Josse et al., 2011; Jørgensen et al., 2011; Lomolino et al., 2016; Mutke et al., 2011; Myers et al., 2000; Ulloa et al., 2017). There are numerous ecological and historical drivers of biodiversity, which may potentially vary among taxonomic groups and geographic areas (Kier et al., 2009). The complex geologic history and current topography of the Andes as well as its influence over the surrounding lands is apparently one of the main promoters of the evolution of range-restricted species with small distributions areas (Arteaga et al., 2016; Duellman, 1988; Lynch and Duellman, 1997). The synergic interactions between geologic, geographic and ecologic factors in NWSA may explain the complex spatial patterns observed in this region (Arteaga et al., 2017; Dodson and Gentry, 1991; Duellman, 1988; Guedes et al., 2018; Jørgensen et al., 2011; Lynch and Duellman, 1997).

Biogeographers have long been drawn towards NWSA to study the origins, patterns and diversification mechanisms that shape the Neotropical biodiversity of this region and, in particular, to the Andes as a model of mountain biogeography. Over the course of a complex 200-year history, scholars have proposed a multitude of frameworks delineating local, national
and international biogeographic regions. (Cabrera and Willink, 1973; Cabrera and Yepes, 1940; Humboldt and Bonpland, 1807; Mello-Leitão, 1937; Morrone, 2014a, 2017, 1999, 2005, 2015; Müller, 1973; Rivas Martínez et al., 2011; Sauer, 1950; Schmarda, 1853a, 1853b; Sclater, 1858; Udvardy, 1975; Wallace, 1876a, 1876b, Dinerstein et al., 1995, 1995; Fittkau et al., 1968). (Plants, birds and mammals have historically been the main biogeographic model group in NWSA and analyses based on such flora and fauna have driven most biogeographic and conservation proposals. Such frameworks have been made possible by intense efforts to create inventories of these groups, whose taxonomy and phylogeny are rather well-understood (Butchart and Bird, 2010; Schipper et al., 2008). However, the study of the spatial biodiversity patterns and biogeographic regionalisation of most vertebrate groups in NWSA remains incomplete. For example, comparatively little is known about less studied groups, such as amphibians and reptiles: amongst such vertebrates, fewer taxa have been described, basic distribution ranges have been poorly delimited and overall less information is available for research and conservation (Bland and Böhm, 2016; Böhm et al., 2013; Howard and Bickford, 2014; Meiri and Chapple, 2016). In the absence of quality data for these groups, global and regional biogeographic regionalisation proposals based on more exhaustively studied animals have frequently been applied without the necessary further validation (Morrone, 2014a).

The aim of the present chapter is to provide a set of multi-taxonomic analyses to reveal region-wide patterns of the biodiversity composition of amphibians, reptiles and birds of NWSA in order to describe and compare their spatial patterns. These data will provide a more complete baseline for the biogeographic regionalisation of NWSA. I base this part of my investigation on a novel database generated for this study that combines a comprehensive, manually compiled distribution dataset for the three study groups. These analyses include: (i) an integrated and updated assessment of the species richness and distribution patterns of more than 3000 species of anuran
amphibians, squamate reptiles and birds; (ii) calculation and comparison of species richness and endemism patterns for the most relevant supra-generic taxa of the studied tax and; (iii) evaluation of the biogeographic regionalisation of NWSA based on the newly-generated data for the studied taxa through cladistics biogeographic methods.

3.2 Methodology

3.2.1 Study area

This study was conducted in the Northern Andes and all adjacent lowland environments in north-western South America (NWSA). A review, definition and description of NWSA is provided in Chapter 1. For further analyses, NWSA will be divided into the following regions: High Andean NWSA (highlands above 1000-1300 m elevation), Trans-Andean NWSA (Pacific and Caribbean lowlands of NWSA) and Cis-Andean NWSA (Amazonian and Orinoquian lowlands of NWSA).

3.2.2 Study taxa and species selection

This study is based on distributional data of three clades of terrestrial vertebrates: anuran amphibians, squamate reptiles and birds. This data originates from a compilation completed in 2015 by the author of this study, which was subsequently adjusted to account for recent taxonomic revisions. I use the terms "reptiles" and “birds” in their classical sense: i.e., reptiles are all non-avian reptiles (including squamates, chelonians and crocodilians), while birds are all avian reptiles.

These groups were selected because of the following motivations: (i) they have been studied extensively and their systematics are fairly well understood; (ii) solved taxonomies allow correct identification of voucher specimens deposited in museum collections; (iii) recently conducted expeditions have significantly increased knowledge about the distribution of most species; (iv)
they show a significant variety of morphological, behavioural, physiological and ecological features, thus representing an interesting heterogeneous group to assess biogeographic patterns on a wide zoogeographic scale and (v) the author of the study has significant taxonomic expertise, field experience and geographic knowledge of all three of these clades in NWSA.

To compile complete species lists of amphibians, reptiles and birds of NWSA, I used the following databases: Handbook of the Birds of the World Alive (del Hoyo et al., 2015), A Classification of the Bird Species of South America (Remsen et al., 2015), The Reptile Database (Uetz and Hošek, 2015) and Amphibian Species of the World: an Online Reference (Frost, 2015). In cases in which different taxonomic hypotheses espoused contradictory views on the nomenclature or definitions of pertinent species, I adopted the most recent evidence-based taxonomic contribution. Subsequently, I selected species that had: (i) at least one valid vouchered record within the geographic boundaries of the study region, with valid vouchers interpreted as verifiable photographs, song recordings or museum specimens; (ii) sufficiently objective and well-defined taxonomic identities so as to be able to assign them valid vouchered records with confidence; (iii) established resident breeding populations in NWSA (so as to exclude all potential populations of species that were migratory, vagrant, or without established populations in NWSA; (iv) locality-points that validate a specific land habitat occurrence (thus excluding all exclusively aquatic species and primarily aquatic or aerial species whose specific locality points cannot be confirmed with certainty given their habitats and modes of movement (e.g. turtles and swifts). I include only well-defined, scientifically described species. Given that the discovery and description of undescribed species continue to increase and that the taxonomic status of such species continues to be modified throughout the course of taxonomic revisions, my dataset represents a snapshot of taxonomic knowledge from 2015 with some updates. The changing taxonomy in some clades, incomplete geographic information and the exclusion of some species at the time of
compilation of my dataset may have resulted in somewhat biased representations of species richness and endemism in some groups but does not invalidate the general patterns herein reported.

Due to the delicate political situation and difficulty in accessing scientific collections in Venezuela, data from species that occur only in that country (either as endemic species or species that reach NWSA by way of this country) could not be included in this study. Thus, all species included in this study are those recorded in the countries of Ecuador and Colombia.

3.2.3 Data collection

I collected species occurrence datasets for each study group: anuran amphibians, squamate reptiles and birds from mainland regions of the Northern Andes. Occurrence data were obtained from different structured and semi-structured data sources. In some cases, some sources were multimodal, involving information from several data modes, including visual, aural, textual and spatial sources. For each occurrence record, I compiled locality-point data and other associated information (see Data structure).

I used the following sources of species occurrence data: (i) scientific literature, (ii) natural history museums, (iii) open data biodiversity databases and (iv) private expert databases. Data extraction from all these sources was conducted between January 2013 and December 2015.

3.2.3.1 Data collection: Scientific literature

I synthesised published species occurrence records based on a literature review I conducted using the library systems of King’s College London and Universidad San Francisco de Quito USFQ, Google Scholar™ scholarly texts search (https://scholar.google.com) and the Biodiversity Heritage Library (http://www.biodiversitylibrary.org). Relevant references were gathered using search terms consisting of “Key taxonomic terms AND Key geographic terms”, where Key taxonomic terms corresponded to scientific and common
names data at the class, family, genus and species level (including synonyms, previous taxonomic classification, and alternative orthographies), and *Key geographic terms* corresponded to geographic names at the country and regional level.

3.2.3.2 Data collection: Natural history museums

I compiled data from the catalogues of museums with actively curated ornithological and herpetological collections. I examined the voucher specimens of all study groups at most museums with Ecuadorian collections. Visits to some museums were conducted prior to this study, but nearly 4500 specimens were examined throughout this dissertation. The following list includes all museums that provided access to their scientific collections (institutional names are followed by their official abbreviations).

(i) American Museum of Natural History, New York, USA—AMNH
(ii) EcoCiencia, Quito, Ecuador—EcoC, housed now at Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador—QCAZ
(iii) Fundación Herpetológica “Gustavo Orcés”, Quito, Ecuador—FHGO
(iv) Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia—ICN
(v) Instituto Nacional de Biodiversidad, Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador—DHMECN
(vi) Instituto Nacional de Recursos Naturales Renovables—INDERENA, Colección de Anfibios; housed now at Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia—IND-AN
(vii) Museo Argentino de Ciencias Naturales, División Herpetología, Buenos Aires, Argentina—MACN
(viii) Museo de Historia Natural “Gustavo Orcés”, Escuela Politécnica Nacional, Departamento de Biología, Quito, Ecuador—EPN
(ix) Museo de Historia Natural, Universidad Nacional Mayor San Marcos, Lima, Peru—MUSM
(x) Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador—QCAZ
(xi) Museo de Zoología, Universidad San Francisco de Quito, Quito, Ecuador—ZSFQ
(xii) Museum National d’Histoire Naturelle, Paris, France—MNHN
(xiii) Museum of Comparative Zoology, Harvard University, Cambridge, USA—MCZ
(xiv) National Museum of Natural History, Washington, D.C., USA—USNM
(xv) Oklahoma Museum of Natural History, Norman, USA—OMNH
(xvi) The Natural History Museum, Department of Zoology, London, United Kingdom—BMNH
(xvii) The University of Kansas, Natural History Museum, Lawrence, USA—KU
(xviii) Universidad de Antioquia, Medellín, Colombia—MHUA
(xix) Universidad del Azuay, Museo de Zoología, Cuenca, Ecuador—MZUA
(xx) Universidad Nacional de Loja, Departamento de Zoología, Loja, Ecuador—LOUNAZ
(xxi) Universidad Técnica Particular de Loja, Museo de Colecciones Biológicas, Loja, Ecuador—MUTPL

For each voucher specimen examined, I obtained all associated data, including information about its locality. I gathered this data from specimen labels, museum catalogues and additional related sources, such as published literature reporting on the museum specimens.
3.2.3.3 Data collection: Open data biodiversity databases

I compiled open data available from the following global databases: Global Biodiversity Information Facility GBIF (GBIF, 2015) for amphibians, reptiles and birds; eBird: An online database of bird distribution and abundance (eBird, 2015), xeno-canto, a website dedicated to sharing bird sounds from all over the world (Xeno-canto Foundation, 2015) and Sistema de Información sobre Biodiversidad de Colombia SIB Colombia (SIB Colombia, 2015) for birds. Relevant occurrence data were gathered using search terms consisting of “Key taxonomic terms”, where Key taxonomic terms corresponded to scientific names at the species level. These data are highly heterogeneous and vouchers are of different types, including preserved specimens and sound vouchers.

In addition, for species with exclusive diagnostic colouration patterns and morphology that facilitate unambiguous identification in photographs, I assembled occurrence data from photograph vouchers in the search engines of Flickr™ (https://www.flickr.com, by Yahoo!), iNaturalist.org™ (http://www.inaturalist.org, by California Academy of Sciences), CalPhotos (http://calphotos.berkeley.edu, by University of California, Berkeley) and Google Images™ search service (https://images.google.com, by Google, Inc.). Relevant images were gathered using search terms consisting of “Genus AND species” or “Common name” where Genus, species, and Common name were replaced by the corresponding data for each species (including synonyms, previous taxonomies and different orthographies).

3.2.3.4 Data collection: Private expert databases

A significant amount of information about the amphibians, reptiles and birds of the Northern Andes remains unpublished and in the private databases of expert herpetologists and ornithologists. In order to collect information kept in private expert databases, I collaborated in the organisation of workshops that brought together herpetologists and ornithologists with expertise on species found in the Northern Andes. During those workshops, each expert
voluntarily provided occurrence records from their private databases, usually obtained through their own field experiences.

Workshops for amphibians and reptiles were part of the global assessments for The IUCN Red List of Threatened Species and were organised in collaboration with The International Union for Conservation of Nature IUCN, NatureServe (with the support from the National Science Foundation’s Dimensions of Biodiversity program, award 1136586), the IUCN-SSC Amphibian Specialist Group, Universidad San Francisco de Quito USFQ and the Asociación Colombiana de Herpetología. I was appointed as Ecuador’s coordinator of the Amphibian Red List Authority and of the Snake and Lizard Reptile Red List Authority. The workshops for birds were part of the national assessments for Ecuador’s Red List of Threatened Species and were organised in collaboration with Aves & Conservación (Birds & Conservation)/ BirdLife in Ecuador, Wildlife Conservation Society, Universidad San Francisco de Quito USFQ and the Ministry of Environment of Ecuador. I was appointed as part of the coordinator committee of the Ecuadorian Red List of Birds. Three workshops were organised to assess squamate reptiles: Medellin, 21–25 October 2013; Quito, 24–27 February 2014 and Quito, 22–26 November 2014; one workshop for amphibians: San Isidro, 16–19 July 2016; and two workshops for birds: 10-13 November 2014, 09–11 March 2016, 01–03 August 2016 and 28 November–01 December 2016. These workshops both updated information for amphibians and birds from previous assessments, also compiled new data and evaluated the information available for all species (see below Data Curation). The reptile workshops were the first comprehensive assessments of the richness and conservation status of reptiles found in NWSA.

In addition to external private databases, I included occurrence records from my own personal database, which includes information about amphibians, reptiles and birds starting in 1998. Specific fieldwork for this dissertation was
completed between 2013 and 2017 and was also included in my personal
database. I organized field trips to areas across Ecuador that were either
poorly represented in museum collections, unexplored or where species’
distribution borders were not validated:

(i) Cotopaxi volcano, province of Cotopaxi;
(ii) Chimborazo volcano, province of Chimborazo;
(iii) Hoya de Chota, different regions including the valleys of Ibarra,
     Urcuquí and San Pablo, as well as the Imbabura volcano, province
     of Imbabura;
(iv) Hoya de Guayllabamba, different regions including valleys of
     Quito, Guayllabamba, Tumbaco, Los Chillos and San Antonio de
     Pichincha, and the Pululahua and Pasochoa volcanoes; province of
     Pichincha;
(v) Hoya de Loja and surrounding slopes, province of Loja;
(vi) Jama to Bahía de Caráquez lowlands, province of Manabí;
(vii) La Maná-Latacunga Pass, and western Andean slopes, provinces of
     Bolívar and Cotopaxi;
(viii) Machalilla National Park and surroundings, province of Manabí;
(ix) Nudo de Pasto, surrounding highland areas on the Páramo de El
     Ángel, and western Andean slopes towards Maldonado;
(x) Papallacta Pass and eastern Andean slopes towards Baeza and
    Coca, province of Napo;
(xi) Pichincha Volcano, province of Pichincha;
(xii) Puyango Protected Forest and surroundings, provinces of El Oro
     and Loja;
(xiii) Tiputini Biodiversity Station, province of Orellana;
(xiv) Zamora and surrounding south-eastern Andes slopes, province of
     Zamora-Chinchipe.
Fieldwork was conducted at all localities mainly by using transects for visual-encounter surveys. Global positioning system receivers were used to position localities and transects, with additional data taken following the standardised suggestions of Riemer (1954) and (Wieczorek et al., 2004). Standardised data were taken for each specimen observed (McDiarmid, 1994). All animals studied were cared for under ethical guidelines (Fellers et al., 1994).

3.2.3.5 Data structure
In order to minimise data heterogeneity, all compiled locality-point data were stored according to the standardised basic record data structure in a Microsoft Excel spreadsheet. The record for each study taxa contains the following fields: (i) scientific name, with the format “genus species”; (ii) locality; (iii) source code (if available, e.g. museum codes or database code); (iv) latitude in decimal degrees; (v) longitude in decimal degrees; (vi) altitude in metres; (vi) source reference and (viii) observations. The fields “locality”, “latitude”, “longitude” and “altitude” were initially filled with the verbatim information available from the original source of the record. Finally, if needed, I modified the contents of these fields according to the data curation protocol in order to lower the amount of data variation, which could ultimately affect its interpretation.

3.2.4 Data curation and data mining
Different sources used for this study provided a significant volume of heterogeneous data. Since most species had few occurrence records (<25 locality-points), nearly every record was critical data. I established a multi-stage protocol for data curation and data mining which facilitated methodological and technological data management support in order to address data quality issues, maximise data use and support future re-use of data. This protocol consists of the following sequential steps: (i) validation of occurrence records, (ii) detection of duplicates, (iii) taxonomic validation, (iv) georeferencing process, (v) preliminary map building, (vi) critical map
assessment, (vi) final map building, (vii) diversity and endemicity analyses and (viii) biogeographic analyses.

3.2.4.1 Data curation: Occurrence records validation
Data provenance was fundamental in determining the trustworthiness of data selected for analysis. I ranked the trustworthiness of data according to the following order: scientific literature, natural history museums, photographic and sound databases, private expert databases and records-only databases (i.e., GBIF and eBird). A standardised annotation mechanism was used to review, evaluate and correct all fields, with relevant annotations of any change reported in the field “observation”. I compiled verbatim geographic information from the original sources, usually available as locality descriptions, museum labels, museum catalogues, field notebooks, online metadata, private database entries, etc. I conducted a preliminary critical evaluation of each record when I collected it from its source in order to confirm that all available information was included and to correct any possible typographical errors. I also read other sections of the source in order to identify additional reported data.

Records without any geographic data (either locality name, references or coordinates) were excluded at this step and coded under “error 3”.

3.2.4.2 Data curation: Duplicate detection
I detected identical occurrence records in the dataset by examining the fields “locality”, “source code”, “source reference” and “observation”. In the case of museum records that were identical with records found in scientific literature, global databases or private databases, I used the museum code to detect duplicates and any possible taxonomic differences between the records. For photographic records, I compared images to detect duplicates. After finding duplicates, I performed a manual comparison of the records in question in order to verify their consistency and completeness. If two records were identical, one was deleted. If records were not identical, I critically evaluated
them in order to determine if they contained unique and pertinent information that could be fused for the analysis, or if they contained incorrect information that indicated that they should be deleted. Records excluded in this step were coded under “error 6”.

3.2.4.3 Data curation: Georeferencing process

I excluded records that had insufficient information to successfully determine the species’ locality. For example, I excluded records that reported only the country (e.g., Colombia) or a general region (e.g., Amazonia) but which contained no additional evidence to allow for a more specific locality restriction. Records excluded in this step were coded under “error 4”.

Records with locality data and coordinates provided directly in the source were validated by confirming whether or not the coordinates accurately matched the described locality. If the coordinates were inaccurate, then the record was coded under “error 1”, but it was not excluded and instead the locality was correctly georeferenced, as described below. Records with locality data but without coordinates were coded under “error 2” and georeferenced, as described below.

I georeferenced all suitable locality-points. In mountainous regions like the Northern Andes, accurate and precise geo-referencing is particularly important because significant altitudinal and climatic changes occur over small horizontal distances. For georeferencing occurrence records, I used the same techniques developed in Cisneros-Heredia (2008). There was a significant variation in the type of point-locality data provided in the records included for analysis. Most sources recorded locality-points as textual descriptions based on distances and directions from places but did not include geographic coordinates. These records were of variable accuracy and quality, and topographic names often evolved over time due to geopolitical and social changes or language mistranslations. Locality coordinates presented indifferent formats such as geographical coordinates or Universal Tranverse
Mercator (UTMs) were available for a limited number of locality-points. Geographical coordinates were converted into decimal coordinates using Google Earth Pro virtual globe software (version 7.1.5.1557, 20 May 2015).

In order to geo-reference occurrence records, I followed a manual protocol involving:

1. I looked for additional relevant information in order to obtain accurate and precise positioning. I reviewed notes from older catalogues, notes on card data files, collectors’ field notes, travel itineraries, information for other non-conspecific specimens collected at the same locality (in sympatry or syntopy) and published articles about sympatric specimens or which were collected on the same fieldtrip. When possible, I contacted the collector to obtain additional information.

2. I determined the position most closely related to the locality-point description and additional information gathered in Step 1 of this protocol by using the collection of maps of Colombia provided by IGAC (2016); the physical map of the Republic of Ecuador (IGM, 2000, 2009, 2011); the geographic map of the Republic of Ecuador (IGM, 2012); gazetteers provided by Brown (1941), Lynch (1979), Lynch and Duellman (1980, 1997) and Paynter, 1993, 1997 and the Geographic Names Database, which contains official standard names approved by the United States Board on Geographic Names and maintained by the National Geospatial-Intelligence Agency (more information available at: http://geonames.nga.mil/gns/html/index.html).

3. I applied the point-radius method (Wieczorek et al. 2004) to determine the area in which the locality is expected to occur by defining an inner point that marks the position most closely related with the locality description and altitude, and a radius that describes the maximum distance from that point (Wieczorek et al. 2004).
4. To minimise variations in data quality which could affect my understanding of the distribution of species across different regions and according to different altitudinal patterns, I included only those occurrence records with uncertainty less than 5 km of linear-length or 200m elevation. Records excluded in this step were coded under “error 7”.

3.2.4.4 Data curation: Taxonomy

Completing correct taxonomic assignment was one of the most demanding and complex processes because it involved exhaustively reviewing the identification of the occurrence records and critically evaluating any inconsistencies or uncertainties that were identified (Bickford et al., 2007; Costello and Wieczorek, 2014; Goodwin et al., 2015; Maldonado et al., 2015; Samy et al., 2013; Soberón and Peterson, 2004). For all records that I curated and approved in previous stages, the following clues were used to detect voucher specimens that had possible taxonomic issues: (i) localities on the borders of the known geographic range of the taxon (including horizontal distribution and elevational range), (ii) suspected or confirmed extra-range localities outside the known geographic range of the taxon; (iii) known species complex characterized by either difficult identifications or fluid taxonomic changes. Each voucher specimen detected using these clues was either borrowed and examined directly by me or was examined by experienced curatorial staff within their respective institutions upon my request specifically for this study. If the identity of the voucher specimen was corrected, the error was coded under “error 5”. Identification was determined using the most updated available taxonomic literature and by comparison with the type series or validated species. In order to identify recent taxonomic changes published in the literature that could affect the taxonomic data curation, I established an event processing method through Google Scholar alerts to track streams of taxonomic data that affect the nomenclature and classification of amphibians, reptiles and birds of NWSA. If the identity remained uncertain due to insufficient taxonomic information, the occurrence
record was excluded and coded under “error 7” (this included specimens suspected to belong to putative undescribed taxa).

3.2.4.5 Data mining: Preliminary map building

Using all validated locality-point records from the previous data curation procedures, I built draft distribution species maps by creating minimum convex polygons in ArcMap using the tool “Point to Polygon – Minimum Bounding Geometry”. The maps represent the extent of occurrence EOO of each species (IUCN, 2012, 2017) and are the first building phase to calculate the Extent of Suitable Habitat (ESH) for each species (Beresford et al., 2011).

3.2.4.6 Data curation: Critical map assessment

Draft distribution species maps were validated by qualitative expert review in two steps. First, I reviewed every map, comparing them with information about species distribution from available literature and my own experience. In particular, I evaluated draft maps in terms of the known geographic and altitudinal species ranges. All problematic localities (i.e., extra-range localities) were reviewed and the curation protocol was repeated. Erroneous localities were excluded.

ESH represent the maximum potential extent of the area of occupancy of a species (Beresford et al., 2011). ESH were proposed as measurement of species range that can reduce commissions errors that are commonly associate with calculations of the extent of occurrence of a species (Beresford et al., 2011; Rondinini et al., 2011). To calculate the ESH of each species, I adjusted the EOO of each species by a deductive approach, which removes the areas outside of the known environmental preferences of the species. I used elevation as a proxy of such environmental preferences. I obtained data on the elevation of each species from the literature and from the assembled validated database produced for this study. Areas outside each species’ elevation limits were not considered as part of the ESH.
The second qualitative expert review was conducted during the workshops (see section Data collection: Private expert databases). During this process, experts confirmed species present in each country and region, verified records available in the database and validated the ESHs. This information was merged with results from similar workshops that have been conducted in other Central and South American countries to produce records for all species with widespread distributions (these records will eventually be published on The IUCN Red List of Threatened Species http://www.iucnredlist.org).

3.2.4.7 Data mining: Final map building

After completing all previous data curation procedures, I used the validated ESH to build the final distribution maps for all species. All maps were generated with GCS WGS 1984 datum.

3.2.4.8 Diversity and endemicity analyses

Species richness (SR) and corrected weighted endemism (WE) were calculated for each study group. SR is the number of species (Lomolino et al., 2016) present in every 1km\(^2\) cell of the entire study area. To calculate SR, in the attributes table of each species polygon I added the column “Value” equaling 1 and converted all polygons into raster using “Value” as the conversion value in ArcMap with the tool “Polygon to Raster” (with 1 km\(^2\) pixel size and WGS 84 Mercator datum). I merged and added all maps for each study group in ArcMap using the Geoprocessing tool “Merge” and the Cell Statistics tool. WE measures endemism by inversely weighting the proportion of endemic species by their range size (species with smaller ranges are weighted more than those with large ranges) and dividing this value by the local species richness (Brown et al., 2016; Crisp et al., 2001; Williams, 2000). To calculate WE, I added another column named “End” in the attribute table of each polygon and input the formula for WE, then added all maps with the Cell Statistics tool.
3.2.4.9 Data mining: Biogeographic analyses

I used the map of biogeographic provinces of NWSA described in Chapter 1, which is based on the proposal by Morrone (2014a, 2017) for biogeographical regionalisation of the Neotropical region. Morrone’s proposal presented a general hierarchical biogeographic classification based on comprehensive cladistics analysis and on biogeographic analyses of terrestrial plant and animal taxa (Morrone, 2014b). However, the spatial resolution of Morrone’s analysis was insufficiently specific for my purposes because it was completed at the level of the whole Neotropical region\textsuperscript{16}. To produce a refined version of Morrone’s proposal, I reviewed each biogeographic province according to the physiographic review presented in Chapter 1, using the best available physiographic information at local, regional and national scales at an optimal resolution of 1 km\textsuperscript{2}. I created this map by refining and modifying Morrone’s proposal by adjusting the borders of each biogeographic province in NWSA with accurate and fine-scale resolution geographic data. This finalized version is suitable for regional and local biogeographic analyses.

Based on the geographic analysis presented in the first part of this chapter, I analysed the lowlands of La Guajira and the highlands of Sierra Nevada de Santa Marta separately given their extensive physiographic differences and in order to test their naturalness (see Chapter 2). The Cauca and Paramo regions were joined together as the Northern Andes region because 1-\textit{km}^2 scale used in this study made it difficult to separate Paramo areas with accuracy. The areas analysed are as follows:

(i) Guajira area: Caribbean lowlands of northern Colombia
(ii) Sierra Nevada area: Highlands of Sierra Nevada de Santa Marta
(iii) Magdalena area: Lower and middle valleys of the River Magdalena

\textsuperscript{16}Morrone’s (2014a) map was converted into shapefile by LöweNeto (2014), but it was equally course and with just 2000 control points across Central and South America.
(iv) Chocó-Darien area: Pacific lowlands of western Colombia and north-western Ecuador
(v) Western Ecuador area: Pacific lowlands of western Ecuador
(vi) Ecuadorian area: Pacific lowlands of southwestern Ecuador and extreme north-western Peru
(vii) Sabana area: Llanos of north-eastern Colombia and Venezuela
(viii) Imerí area: Amazonian lowlands of eastern Colombia
(ix) Napo area: Amazonian lowlands of eastern Ecuador, south-eastern Colombia and extreme north-eastern Peru
(x) Yungas area: Inter-Andean basin of Zumba in the southern Andes of Ecuador
(xi) Northern Andes area: Northern Andes of Colombia and Ecuador.

I analysed 3144 taxa, including species of anuran amphibians, reptiles and birds. All these species inhabit NWSA, although some of them also inhabit other regions. Merged distribution maps of each study group were cut according to the biogeographic provinces in order to understand species richness patterns within each biogeographic area. Then, the distribution map of each taxon was used to automatically allocate it to the different analysed areas using a geographical information system in ArcGis® 10.4 by ESRI. A data matrix was constructed, with rows representing species’ presence/absence and columns representing the areas analysed. Each entry was coded as either “1” or “0”, depending on whether the species range coincided with the analysed area. Expert consistency review was applied in order to check for species that could have been erroneously assigned to an area—mainly due to the scale of the analysis. This step was particularly relevant for mountain areas. A hypothetical unit coded as all zeros was added to the matrix in order to root the resulting cladograms. Two different analyses were performed: (i) a parsimony analysis using the software PAUP (Phylogenetic Analysis Using Parsimony), version 4.0 (Swofford, 2003), setting Goloboff concavity $k = 0$, and (ii) Unweighted Pair Group Method with
Arithmetic Mean (UPGMA), using the Jaccard coefficient, with program, DendroUPGMA (García-Vallvé and Puigbo, 2017; García-Vallvé et al., 1999), following recommendations by Kreft and Jetz (2010) and Morrone (2009, 2017).

3.3 Results

3.3.1 Data description and quality assessment

A total of 1075 species of anuran amphibians are reported to occur in the Northern Andes, with 755 species in Colombia and 557 in Ecuador through June 2017. With the inclusion of 26 species of salamanders and 41 species of caecilians, the overall list of amphibians analysed in this study includes 1142 species inhabiting the Northern Andes. The most diverse clades within Anura are Brachycephaloidea with 39% of the species, followed by Hylidae (16%), Dendrobatoida (13%) and Bufonidae (11%). The most speciose genera are Pristimantis and Dendropsophus. The same regional patterns are apparent when each country is analysed separately. There are at least 674 species of anurans that are endemic to NWSA. There are 362 species of anurans that are geopolitically endemic to Colombia and 207 to Ecuador. In 2015, when species data collection was closed, 914 species were used for analyses developed in this chapter.

A total of 711 species of squamate reptiles (herein referred to simply as “squamates” for brevity) are reported to occur in the Northern Andes, with 510 species in Colombia and 426 in Ecuador as of June 2017. With the inclusion of 45 species of turtles and 6 species of crocodilians known to occur in the Northern Andes, the overall list of non-avian reptiles contains 762 species inhabiting the Northern Andes. The most diverse families within Squamata are Colubridae (40%), followed by the clade Iguania (22%) and Gymnophthalmidae (12%). The most speciose genera are Anolis and Atractus. The same regional patterns are apparent when each country is analysed.
separately. There are 278 species of squamate reptiles that are geopolitically endemic to Colombia and 204 to Ecuador. In 2015, when species data collection was closed, 564 species were used for analyses developed in this chapter.

A total of 2141 species of birds are reported to occur in the Northern Andes, with 1963 species in Colombia and 1621 in Ecuador through June 2017. Due to amount of data, analyses with birds were done at the taxonomic level of class only. In 2015, when species data collection was closed, 1762 species were used in this chapter.

The database of validated records included 42278 locality-points, divided between 23003 locality-points of birds, 8712 of squamate reptiles and 10563 anuran amphibians. A total of 6297 locality-points were corrected, validated and included (14% of all validate-records), while 2171 locality-points were excluded due to errors. The most common errors for all groups were due to taxonomic problems and uncertainty (errors 5 and 7) and by quality of geographic positioning data (errors 2, 1 and 3). For birds, a high number of errors were related to geographic uncertainty of records provided by experts (error 7). The sources with highest number of errors were open date online databases and museum catalogues. In both sources, the most common errors were related with taxonomy (error 5) and lack of georeferenced data (error 2). GBIF data was the most contaminated source (75% of the errors), while eBirds, xeno-canto and the photographic online database had more accurate records. Errors found in data gathered from the literature were mainly related to duplicated records (error 6), due to use of specimens in different publication) and lack of georeference data (error 2). Errors in data provided by experts were mainly due to taxonomic problems (error 5) related to insufficient information updating and record curation.
One of the most challenging issues to solve was incorrectly identified specimens which contaminated distributions patterns by introducing erroneous locality-points.

Despite curatorial work at museum collections, more than 1200 specimens were not included in this study due to pending taxonomic investigations. Using the protocol established in this study, I was able to correctly identify 4076 specimens. I participated in the discovery and description of 22 new taxa based on data produced during the development of this dissertation. These newly described taxa are populations that were either (i) previously part of species-complexes that alpha-taxonomy helped to identify as different evolutionary entities or (ii) populations of species that were discovered and described by science for the first time. (Appendix 1). In addition, I created 27 species distribution reviews based on the extensive taxonomic and geographic studies conducted (Appendix 1)

3.3.2 Species richness spatial patterns in NWSA

Amphibians: The highest anuran SR (118 spp.) was in the evergreen forests of the Amazonian lowlands of eastern Ecuador, south-eastern Colombia and northeastern Peru. Anuran SR is higher in lowland areas (Trans- and Cis-Andean) which are characterised by higher yearly rainfall and non-seasonal rainfall patterns. Areas with the highest anuran SR are mainly found in the Upper River Napo basin on the Amazonian lowlands of north-eastern Ecuador, the Pacific lowlands of north-western Colombia and north-western Ecuador, the Andean slopes of the Cordillera Occidental of Colombia and northern Ecuador and the Andean slopes of Cordillera Real of Ecuador.

Maximum anuran SR in the Cis-Andean region (118 spp.) is about 50% higher than maximum anuran SR in the Trans-Andean region (59 spp.). Maximum anuran SR in the Cis-Andean region is also higher than in the High Andes (69 spp.). Trans- and High Andean SR are similar, but the latter is slightly greater
(17%). In the Cis-Andean region, SR decreases with altitude around the Andean foothills and slopes. SR also decreases with latitude, from the Upper Napo River basin to the north, drastically across the River Caquetá, and, more gradually towards the grasslands of the Llanos. SR across the Amazonian lowlands is not uniform, and the highest SR is found in the Upper Napo basin, next to the Andes. SR gradually declines across most north-eastern Peru and south-eastern Colombia and then increasing on the Iquitos-Leticia area. Trans-Andean SR is higher in the evergreen forests of western Colombia and north-western Ecuador and decreases with altitude. This decrease is less marked than in Cis-Andean areas, but drastically declines in the northern and southern areas, across seasonal semideciduous and dry forest of the Caribbean lowlands in La Guajira and the lower River Magdalena valley, as well as in the Pacific lowlands of western Ecuador and extreme north-western Peru. Anuran SR in the seasonal evergreen forests of the Caribbean lowlands is lower than in the Pacific lowlands, but the dry forests of the Caribbean and Pacific lowlands show similar anuran SR. SR across the rainforest of the Pacific lowlands is not uniform, and the highest SR values are found in north-western Colombia. SR gradually declines across south-western Colombia, but then increases in the Andean foothills and surrounding lowlands of north-western Ecuador. While SR is prevalent throughout all of the lowlands and coastlands in north-western Colombia, in south-western Colombia and north-western Ecuador, SR increases around the Andean foothills and declines near the coastlands. These SR changes seem to be related with the climatic patterns, caused by the lower humidity prevalent in south-western Colombia between the rivers San Juan and Patia and to the south of River Esmeraldas in north-western Ecuador.

High Andean SR shows a non-continuous pattern, with higher SR in the cloud forests on the western slopes of the Cordillera Occidental of Colombia and north-western Ecuador, on the eastern slopes of Cordillera Oriental of Ecuador and nearby isolated mountain ranges and, to a lower degree, in the
central Magdalena River Valley. Lower SR from central and southwestern slopes of Cordillera Occidental of Ecuador and across Cordillera Central of Colombia probably reflects a real pattern—related to lower humidity. However, lower SR along the eastern slopes of Cordillera Oriental of Colombia most probably reflects incomplete species and localities sampling. SR in the Sierra Nevada de Santa Marta and the extreme southern valley of the River Marañon (which barely enters NWSA) are significantly lower than in the Northern Andes. High Andean SR declines with altitude towards the paramos. Anurans are more diverse in cloud forests than at higher altitudes across the Andes of Colombia. However, in the Andes of Ecuador, anurans show higher SR at higher elevations from the southern Nudo de Pasto to the Nudo de Azuay located on the Cordillera Occidental, and south of the Contrafuertes of Tzunantza and Nanquipa, on the Cordillera Real. Anuran SR drastically declines in extreme southern Ecuador, south of Nudo de Azuay and of the Contrafuerte de Tzunantza.

A closer look at independent clades of amphibians suggests that high Cis-Andean SR is mainly caused by species of Hylidae (genera *Dendropsophus* and *Boana*), Terrarana (genus *Pristimantis*), Leptodactylidae (genus *Leptodactylus*) and Dendrobatidae. However, SR peaks do not fully coincide among these groups, with Hylidae and Terrarana showing higher SR closer to the Andes, while Leptodactylidae and Dendrobatidae show a more even pattern along the Amazonian lowlands of Ecuador and Peru, with higher peaks around the Iquitos area. The clade Pipidae is entirely restricted to Cis-Andean regions. Trans-Andean SR is dominated by species of the clades Terrarana (genus *Pristimantis*), Centrolenidae and Dendrobatidae. In the High Andes, Terrarana, Centrolenidae, Dendrobatidae and Hemiphractidae (genus *Gastrotheca*) are the dominant clades contributing to the region’s SR. The clade Terrarana, with its leading genus *Pristimantis*, has the widest distribution and most even SR pattern among all clades, attaining high SR both in the Cis- and Trans-Andean lowlands and on the Andean slopes. Most clades of
amphibians have low SR in the High Andes (Bufonidae, Ceratophrydae, Dendrobatoidea, Hylidae, Leptodactylidae, Microhylidae, Pipidae, Ranidae), but two clades (Telmatobiidae and Hemiphractidae) are mostly or completely found in the highlands.

Reptiles: The highest squamate SR is found across the evergreen forest of the Amazonian lowlands in Colombia, eastern Ecuador and eastern Peru. Cis-Andean SR declines with altitude around the Andean foothills and slopes, and also gradually heading towards the area of Los Llanos in Colombia and Venezuela. SR across the Amazonian lowlands is fairly uniform, showing gradually increasing values towards the most eastern part of the Napo River and Putumayo river basins in the Iquitos-Leticia area.

Maximum squamate SR on the Trans-Andean region also shows important levels of squamate SR, but with about 30% less species than in the Cis-Andean region. Trans-Andean SR shows a fairly uniform pattern across the Pacific lowlands of western Colombia and north-western Ecuador. SR gradually declines near the seasonal deciduous and dry forests of western Ecuador. Squamate SR in the seasonal evergreen forests of the lower River Magdalena Valley is slightly lower than SR in the Pacific lowlands, gradually declining along dry forests of the La Guajira, which have lower squamate SR than dry forests of the Pacific lowlands of Ecuadorian. SR across the Pacific lowlands of Colombia and Ecuador is fairly uniform, with slightly higher SR in the river basins of Atrato-Baudó-San Juan, Calima-Anchicayá-Cajambre and between the rivers Mira and Santiago. Across the Pacific lowlands, SR is prevalent on the entire lowlands and coastlands, but towards western Ecuador, SR is more strongly concentrated near the Andean foothills and declines in the coastlands. Although similar to anurans, this trend is less marked in squamates, which are more widespread and in higher species richness in the drier coastlands.
In the High Andes, maximum squamate SR is similar to Cis-Andean SR, and lower than maximum Trans-Andean SR. High Andean SR shows a non-continuous pattern, which is fairly different from that observed in amphibians. Higher SR occurs mainly in the large valleys of the rivers Cauca and Magdalena and is much more restricted to the cloud forests on the western slopes of the Andes of south-western Colombia and north-western Ecuador, and on the eastern Andean slopes and nearby isolated mountain ranges of Ecuador. When compared with anurans, squamates show a rather inverse pattern, with higher SR values at higher altitudes across all highlands of Colombia, including the Andes, isolated surrounding mountain ranges, and Sierra Nevada de Santa Marta and lower SR across the highlands of Ecuador. The exception occurs in southern Ecuador, where squamates show higher SR values to the south of the Nudo de Azuay, specifically in the valleys of the rivers Jubones and Catamayo. High SR is also found south of the Contrafuerte de Tzunantza, in the valleys of the rivers Nangaritza and Mayo and the nearby mountain ranges (i.e., contrafuertes of San Francisco, Paredones and Lagunillas).

A closer look at independent clades of squamates suggest that high Cis-Andean SR is mainly caused by species of Colubridae, and to a lesser degree, Iguania and Gymnophthalmidae. However, SR peaks do not fully coincide among these groups, with Colubridae attaining higher SR near central Amazonia, Iguania near western Amazoni and Gymnophthalmidae with a fragmentary pattern between western and central Amazonia. The clades Aniliidae, Sciencidae and Typhlopidae are mostly or entirely restricted to Cis-Andean regions, while the clades Anguidae and Tropidophidae are mostly or entirely restricted to Trans-Andean regions. Trans-Andean and High Andean SR is dominated by species of the clades Iguania and Colubridae. The clades Colubridae and Iguania are the most widespread along the Northern Andes and are the only squamate clades that inhabit higher elevations (mountains over 1900 m) in the High Andean regions, although their distribution patterns
differ significantly. Colubrid exhibits greater SR in Cis-Andean regions than in Trans-Andean regions, while Iguanian SR is fairly similar on both sides of the Andes. Iguanian also inhabits higher elevations (up to the paramo, over 4000 m) than Colubridae.

Birds: The highest SR amongst birds was found in the evergreen forests of the Amazonian lowlands of Ecuador, south-eastern Colombia and north-eastern Peru and distinctively on the Serranía de Perijá, Colombia. Bird SR is higher in lowland areas (Trans- and Cis-Andean), but an association with climatic patterns is not as well defined as it is in anurans and squamates.

Maximum bird SR occurs on the borders between the Cis-Andean and High Andean region in Ecuador (520 spp.) and is about 3.6–4% higher than maximum bird SR in the lowlands of the Cis-Andean region (502 spp.) and in the High Andes (499 sp.), and 15% higher than bird SR in the Trans-Andean region. In the Cis-Andean region, avian SR is particularly high along the Andean foothills and adjacent Amazonian lowlands of eastern Ecuador and south-eastern Colombia. Further east, SR shows a distinct pattern, with high SR along the Napo, lower Marañon, Pastaza and Amazonas riverine areas. Cis-Andean SR declines with altitude towards the Andean slopes, towards the Amazonian lowlands of central-eastern Colombia, and, drastically, across Los Llanos of Venezuela and Colombia in the Orinoquian lowlands. In general, the heterogeneity of Cis-Andean SR probably reflects a real biogeographic pattern related to the complexity of Amazonian ecosystems and rivers that generate a matrix between forest and riverine communities, both of which are inhabited by range-restricted species. Trans-Andean SR is higher in the foothills of Serranía del Perijá and Sierra Nevada de Santa Marta, as well as in the humid forests of the Caribbean and Pacific lowlands of the Darién region. SR across the Pacific lowlands of western Colombia and north-western Ecuador show moderate SR (250–300 spp.), with slightly higher SR in the foothills of Cordillera Occidental of Colombia between Cerro Calima and
Farallones de Cali, and on the Montañas de Mache and Motañas de Chindul of Ecuador. Bird SR is lower between the Patia and San Juan rivers, and also declines gradually towards the seasonal and drier areas of southwestern Ecuador and of La Guajira. SR in the Pacific lowlands of Colombia and Ecuador show a rather composite pattern in which climatic associations are not directly apparent.

The greatest SR in the High Andean regions is on the Sierra Nevada de Santa Marta, Serranía del Perijá, Serranía de San Lucas and the Andean slopes of the Cordillera Oriental in southern Colombia and the Cordillera Real of Ecuador (especially on the Sub-Andean areas). Higher SR is also concentrated in the cloud forests of the River Cauca valley and the Cordillera Central of Colombia, as well as on the eastern Andean slopes of the Cordillera Oriental of northern Colombia. SR declines markedly with elevation and the highlands show a rather continuous pattern of SR decline across the Cordillera Occidental of Colombia and Ecuador and across the Upper River Magdalena Valley.

3.3.3 Endemism spatial patterns in NWSA

Amphibians: The highest SR of endemic anurans of Colombia and Ecuador is found in the foothills and slopes of Cordillera Occidental of Colombia and north-western Ecuador, in the adjacent Pacific lowlands, in the Amazonian lowlands and foothills and on the slopes of the Cordillera Oriental of Ecuador. Endemic anurans exhibited lower SR in the lowlands, foothills and the slopes of central-western Ecuador and northern Colombia. There is no significant correlation between general species richness and endemic species richness ($r^2 = 0.23$, $p > 0.05$).

The high values of WE of anuran amphibians show a patchy pattern across all of the mountain ranges of north-western South America, including the Cordillera Occidental of Colombia, Cordillera Central and Cordillera Oriental of Colombia as well as the Cordillera Occidental and Cordillera Real of
Ecuador. In these regions, the highest endemism values were found on the mountain peaks and montane slopes. Other isolated mountain ranges not part of the Andes, also show high endemism values. These include the Sierra Nevada de Santa Marta of Colombia and the Cordillera de Chilla, Cordillera Guacamayos-Napo-Galeras, Cordillera del Kutuku and the Cordillera del Condor of Ecuador. Mid WE values were detected in lowland and foothill areas immediately adjacent to the Andes in south-eastern Colombia and eastern Ecuador (between the River Caquetá in Colombia and the headwaters of River Santiago in Ecuador), in south-western Colombia and north-western Ecuador (between the River San Juan, Colombia and the River Esmeraldas, Ecuador), and next to the isolated mountain ranges of Serranía de la Macarena and Serranía de Chiribiquete, Colombia and the Cordillera de Chilla, Cordillera de los Guacamayos-Napo-Galeras, and Cordillera de Kutuku, Ecuador. Along the lowlands closer to the ocean, WE values are usually low, with the exception of the delta of the River San Juan and the lowlands around the lower basins of the rivers Calima, Anchicayá, Cajambre and Naya in central-western Colombia; the lowlands in Cabo Pasado, Cabo San Lorenzo, Punta Salango and the Gulf of Guayaquil in Ecuador; and the lowlands and foothills of the River Catamayo valley and adjacent Celica and Sozoranga mountains of Ecuador.

Reptiles: The highest SR of endemic squamates of Colombia and Ecuador is found in the Pacific lowlands as well as on the slopes and foothills of the Cordillera Occidental of Ecuador, declining towards southwestern Colombia. It also peaks in the Upper River Pastaza basin, in the foothills of the Cordillera Oriental and in the immediately adjacent Amazonian lowlands. There is no significant correlation between general species richness and endemic species richness ($r^2 = 0.12, p > 0.05$).

High values of WE for squamates show a patchy pattern across the mountain ranges of the Andes in Colombia and Ecuador and across other isolated
mountain ranges. Areas with high WE are smaller than those observed in amphibians. The Andean slopes to the west of the Pichincha Volcano show a constant pattern of high WE in anurans and squamates. In addition, high WE values are exhibited in areas where amphibian endemism was lower: Pacific lowlands of western Ecuador, between the Mira River and the Tumbes River. WE of reptiles is high on the Montañas de Mache, and on the lowlands of Guayas and El Oro. High endemism is also present in the Andes of southern Ecuador, across the Macizo del Cajas, Nudo de Portete, Cordillera de Chilla, Páramos de Matanga, Cordillera de Cordoncillo, Contrafuerte de Tzunantza and in the Zumba-Marañon Valley. Mid-values of squamate WE are exhibited in the seasonal evergreen and semideciduous forests of western Ecuador, deciduous forests of south-western Ecuador, the area of Buenaventura, the River Calima region of central-western Colombia, the slopes of Sierra Nevada de Santa Marta and in patchy areas on the northern Andean slopes of the Cordillera Occidental, Central and Oriental of Colombia.

Birds: The highest SR of endemic birds in Colombia and Ecuador is found in the Andean foothills, on the slopes of the Cordillera Occidental of Colombia and Ecuador, and in the Pacific lowlands of western Colombia and north-western Ecuador. Mid-levels of endemic bird SR are also observed in the Pacific lowlands of western Ecuador and along the highlands, especially the Cordillera Real. There is no significant correlation between general species richness and endemic species richness ($r^2 = 0.08, p > 0.05$).

High values of WE for birds show a continuous pattern across all Andean mountain ranges of Colombia and Ecuador (including the Cordillera Occidental, Cordillera Central and Cordillera Oriental of Colombia and the Cordillera Occidental and Cordillera Real of Ecuador), as well as in the River Cauca Valley and in the Upper River Magdalena Valley. The top values of WE are exhibited in the northern and central parts of the Cordillera Central of Colombia, in the northern and central parts of Cordillera Oriental of
Colombia, on the Serranía del Perijá and on the Andean slopes of the Cordillera Real of Ecuador. Mid-values of WE are observed on Sierra Nevada de Santa Marta, the Pacific lowlands and Andean foothills of southern Colombia and northern Ecuador, the Andean foothills of south-western Ecuador and in the Pacific lowlands of extreme southern Ecuador and northern Peru. In the Cis-Andean region, WE is lower than in other areas, but there are higher WE values observed closer to the Andes and along the Marañon and Amazonas rivers, and also slightly higher towards Los Llanos of northern Colombia.

### 3.3.4 Biogeographic regionalisation

The presence or absence of each of the studied species in the different biogeographic provinces is summarized in Appendix 9. Topology of UPGMA dendrograms show consistent results across all study groups when analysed separately or combined (Figures 2, 3, 4, 5). In all cases, Yungas is the most different biogeographic province, diverging basally from all other groups. Two clades were recovered in all UPGMAs, one in Cis-Andean biogeographic provinces and another in Trans-Andean biogeographic provinces. For all groups, the Sabana regions clusters with the Trans-Andean provinces. The clade composed by Sierra Nevada and Guajira usually clusters with the Trans-Andean provinces, but it clusters basally to all regions (except for Yungas) in the UPGMA of amphibians. UPGMAs of birds and reptiles show distances between Sierra Nevada and Guajira as large as those observed between other well-established biogeographic provinces (e.g., Western Ecuador and Ecuadorian, or Sabana and Imeri). The Northern Andes are not stable across the the UPGMA analyses. The Northern Andes cluster with the Trans-Andean provinces in UPGMAs of amphibians and reptiles, but with the Cis-Andean provinces in UPGMAs of birds and with all groups combined. Phylograms obtain through parsimony analysis show more complex topographies than UPGMA dendrograms (Figures 6, 7, 8, 9). The most parsimonious tree for all
groups combined shows the biogeographic provinces of the Pacific lowlands, Guajira–Sierra Nevada and Sabana–Imeri clustering together as monophyletic units. Sabana and Imeri are separated from Napo by Magdalena and the Northern Andes. Phylograms for reptiles shows similar patterns, with biogeographic regions from the Pacific lowlands clustering together and including Yungas, apparently due to species shared between the dry forests of the Ecuadorian and Yungas provinces. Guajira and Sierra Nevada are not clustered together, but they are subsequent basal branches to a clade formed by the three Trans-Andean biogeographic regions (Imeri–Napo–Sabana). The cladogram for birds shows Magdalena as basal to all other regions, Sierra Nevada and Guajira forming a clade, and the biogeographic regions of the Pacific lowlands basal to a clade formed by the biogeographic regions of the Trans-Andean region together with Yungas and Northern Andes. The phylogram for amphibians shows low resolution: most branches are almost collapsed and strong cladistics signal is not apparent. In general, these analyses show, or at least do not conflict with, a separation between Cis-and Trans-Andean regions, clustering of Pacific lowland regions separately from Caribbean lowland regions, the distinctiveness of Sierra Nevada from Guajira, the closer relationships between Sabana and the Cis-Andean regions and the unstable position of Northern Andes.
Cophenetic Correlation Coefficient (CP) = 0.827149169406944. Newick tree format:
(((Choco:0.231,Magdalena:0.231):0.072,(Ecuadorian:0.175,WesternEcuador:0.175):0.128):0.041,(Guajira:
0.139,SierraNevada:0.139):0.204):0.018,((Imeri:0.203,Sabana:0.203):0.094,(Nandes:0.258,Napo:0.258):0.039):0.065):0.030,Yungas:0.392);

Figure 2: UPGMA dendrogram based on the Jaccard coefficient between biogeographic regions of north-western South America with data of amphibians, reptiles and birds.
Cophenetic Correlation Coefficient (CP) = 0.792014671143744. Newick tree format:
((((Choco:0.158,Magdalena:0.158):0.096,(Ecuadorian:0.143,WesternEcuador:0.143):0.110):0.051,(Guajira :0.123,SierraNevada:0.123):0.182):0.013,((Imeri:0.177,Sabana:0.177):0.049,(Nandes:0.179,Napo:0.179):0.0 47):0.092):0.039,Yungas:0.357)

Figure 3: UPGMA dendrogram based on the Jaccard coefficient between biogeographic regions of north-western South America with data of birds.
Cophenetic Correlation Coefficient (CP) = 0.906811994499582. Newick tree format:

((((((Choco:0.291,Nandes:0.291):0.033,Magdalena:0.324):0.053,(Ecuadorian:0.183,WesternEcuador:0.183):0.194):0.038,(Guajira:0.218,SierraNevada:0.218):0.197):0.016,((Imeri:0.207,Sabana:0.207):0.052,Napo:0.260):0.172):0.042,Yungas:0.473).

**Figure 4:** UPGMA dendrogram based on the Jaccard coefficient between biogeographic regions of north-western South America with data of squamate reptiles.
Cophenetic Correlation Coefficient (CP) = 0.872826180405463. Newick tree format:

(((Choco:0.343,Nandes:0.343):0.062,Magdalena:0.405):0.024,(Ecuadorian:0.323,WesternEcuador:0.323):0.106):0.038,((Imeri:0.327,Napo:0.327):0.057,Sabana:0.384):0.083):0.008,(Guajira:0.198,SierraNevada:0.198):0.277):0.014,Yungas:0.489).

**Figure 5:** UPGMA dendrogram based on the Jaccard coefficient between biogeographic regions of north-western South America with data of anuran amphibians.
Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America, based on species of anuran amphibians, squamate reptiles, and birds. This was the most parsimonious tree among 5000 trees. Number of species/characters = 3144, constant characters = 72, variable characters that are parsimony-uninformative = 638, parsimony-informative characters = 2434, tree length = 6084, consistency index (CI) = 0.500 (excluding uninformative characters = 0.443), retention index (RI) = 0.426, rescaled consistency index (RC) = 0.213, homoplasy index (HI) = 0.500 (excluding uninformative characters = 0.558).

Figure 6: Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America
Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America, based on species of birds. This was the most parsimonious tree among 5000 trees. Number of species/characters = 1666, constant characters = 68, variable characters that are parsimony-uninformative = 239, parsimony-informative characters = 1359, tree length = 3455, consistency index (CI) = 0.463 (excluding uninformative characters = 0.423), retention index (RI) = 0.457, rescaled consistency index (RC) = 0.211, homoplasy index (HI) = 0.538 (excluding uninformative characters = 0.577).

**Figure 7**: Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America
Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America, based on species of reptiles. This was the most parsimonious tree among 5000 trees. Number of species/characters = 564, constant characters = 4, variable characters that are parsimony-uninformative = 125, parsimony-informative characters = 435, tree length = 1025, consistency index (CI) = 0.546 (excluding uninformative characters = 0.483), retention index (RI) = 0.473, rescaled consistency index (RC) = 0.259, homoplasy index (HI) = 0.454 (excluding uninformative characters = 0.517).

**Figure 8:** Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America
Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America, based on species of amphibians. This was the most parsimonious tree among 5000 trees. Number of species/characters = 914, constant characters = 0, variable characters that are parsimony-uninformative = 274, parsimony-informative characters = 640, tree length = 1482, consistency index (CI) = 0.617 (excluding uninformative characters = 0.530), retention index (RI) = 0.455, rescaled consistency index (RC) = 0.281, homoplasy index (HI) = 0.383 (excluding uninformative characters = 0.470).

**Figure 9:** Topology of phylogram depicting the relationships of the biogeographic provinces of north-western South America
3.4 Discussion

3.4.1 Overview

This study provides insights into the spatial patterns of amphibians, reptiles and birds in NWSA, based on distributional data of about 83% of the known described species from the region. Data presented herein constitutes the most extensive and complete curated dataset currently available for these three groups from the region, both in geographic coverage (number of locality-points) and taxonomic coverage (number of species). This study provides information on how the communities of these terrestrial vertebrates are structured in space and demonstrate the importance of well-curated data. Previous studies of spatial biodiversity patterns in South America have usually analysed much larger areas but with coarser spatial resolutions and less species data (e.g., Morrone, 2006; Ron, 2000), have reconstructed distribution areas based mainly on expert opinion (e.g., Albuja et al., 1980; Hernández-Camacho et al., 1992), have used only partial sets of taxa (e.g, Avila-Pires et al., 2009; Navarrete et al., 2016), have focussed on specific biomes (e.g., Porzecanski and Cracraft, 2005) and have analysed traditional or geopolitical areas, defined without full consideration of their historical and ecological coherence and synergies (Da Silva et al., 2005; Juen and Marco, 2012). The study presented herein is the first step to understanding the spatial biodiversity patterns and biogeography of one of the most historically complex, ecologically diverse and highly human-impacted regions in the world. This study is the first overview and establishes a baseline for future work that will use more exhaustive analyses to reveal further evidence of evolutionary and biogeographic phenomena.

3.4.2 Limitations and Data quality

I am aware of limitations in the dataset, methods and results of this study. After data extraction was finished in December 2015, several new distribution
records were published or became available in museums and online databases. Most of those records will lead to future modifications of minor aspects of the distribution maps of some taxa (e.g., frogs of the genus *Pristimantis* from the High Andes (Brito et al., 2017) or *Dipsas* from the Pacific lowlands (Arteaga et al. in review)), but should not greatly impact the patterns described in the results. However, some records will be significant and may change the endemicity interpretation for some species (e.g., (Jaramillo-Martinez et al., 2015; Martínez and Serrano-Cardozo, 2017), but should not affect general spatial patterns or biogeographic regionalisation. One of the biggest limitations in all studies dealing with biodiversity is taxonomic uncertainty.

Geographic precision across the study was based on a 1-km² resolution, but such a spatial scale hides significant details in mountainous areas, where significant abiotic and biotic changes may occur inside 1 km². Joining together all High Andean regions was not optimal but reduced the probability of wrongly assigning records in highly mountainous/inclined areas. Temporal information was not included as a variable in this study in order to include the full dataset of species and distribution records. Additionally, many records are not precisely dated, thereby limiting the direct application of this dataset to the study of impacts of climate change and habitat change over time. All analyses rely on distribution maps derived from adjusted minimum convex polygons based on specific locality-point records, which extrapolate the species range over the intervening areas where species records are expected, but this method may overestimate or underestimate species distribution ranges depending on sample size, habitat heterogeneity, the magnitude of errors during georeferencing and sampling effort (Burgman and Fox, 2003). Biodiversity sampling efforts in Colombia and Ecuador are uneven, and a large amount of species records come from accessible areas near roads or urban centres, while far less information is available for isolated or disconnected areas (Sierra et al., 2002). However, in recent years, this trend
has begun to gradually change due to increased road access to previously undisturbed areas and due to a greater collection efforts in Colombia and Ecuador (e.g., Almendáriz et al., 2014; Brito et al., 2017; Brito M. and Pozo-Zamora, 2013; Renjifo et al., 2017). Furthermore, due to the necessary changes between shapefile and raster format, some resolution is lost, thereby further increasing the probability of over-prediction of species’ ranges. Due to all these factors, SR is likely exaggerated in some areas. However, since such bias is equally likely for all species and a large number of species was evaluated, I expect that general trends and patterns as well as observed differences are reliable. I am also convinced that the results presented herein show natural patterns. In fact, several of the SR and endemicity centres found in this study coincide with regions (e.g., Choco-Darién) that have been recognised and remained stable in basically all studies that have analysed spatial patterns in tropical America (Morrone, 2017), despite differences in the total number of species, included taxa and methodological approaches. Furthermore, the disparity of patterns among different clades of birds, reptiles and amphibians are a strong signal that major bias is not present.

The quality of any analysis depends on the quality of data analysed. Data curation and data mining protocols were the cornerstone of this study. Although time consuming, these processes allowed me to filter data and increase data quality in complex, diverse and heterogeneous groups. Data provided by experts and obtained from the literature usually had fewer errors and was easier to process. Interestingly, the biggest exception in this case was expert data for birds. Bird data provided by experts encompassed a larger level of uncertainty because of taxonomic and geographic reasons, as compared with similar data for amphibians and reptiles. I hypothesize that the main reasons behind these uncertainties are related to the professional differences between people working with the different study groups. In Ecuador and, to a lower degree, in Colombia, available experts on birds were usually not professional ornithologists, but rather birdwatchers. Less than 15
ornithologists are active in Ecuador on a regular basis, while there are over 200 amateur birdwatchers and professional tourism-oriented birdwatchers. Data provided by birdwatchers (directly as experts or through online databases) consistently had higher number of geographic and taxonomic errors (not just in terms of the species identification, but also in terms of a lack of taxonomic updates due to the consistent use of English-only names). I do not intend to deny or question the importance of birdwatching for science and conservation with these observations (Sullivan et al., 2009; Wiersma, 2010; Wood et al., 2011), but rather to highlight the importance of an adequate partnership between ornithologists and birdwatchers, who can collaborate to produce better scientific data. Data obtained from online databases (especially GBIF) have a significant amount of taxonomic and geographic errors. This problem has been extensively discussed and comprehensive data cleaning procedures need to be implemented to improve this data quality (Constable et al., 2010; Gueta and Carmel, 2017; Webster, 2017). However, in addition to curation procedures once the data is online, the first step that should be urgently implemented is promoting the training of taxonomists so that they can correctly identify and describe species. Despite wide recognition that taxonomy is key to all fields related with biodiversity, an alarming decline in the education and professionalization of taxonomists is evident, even in natural history museums (de Carvalho et al., 2014; Hopkins and Freckleton, 2002; Vogel Ely et al., 2017; Wheeler, 2004). This trend is not constant across all taxonomic groups. For example, amphibians became a highly studied group after the severe global population declines that began to be reported since the 1980s and 1990s, which boosted the amount of discovery and description of species, thereby ultimately improving the quality of biodiversity data for this group of vertebrates (Köhler et al., 2005). However, reptiles are basically a neglected group, with very few people studying their taxonomy. There are a large number of Data Deficient species, despite studies demonstrating global declines of many reptiles (Bland and Böhm, 2016; Böhm
et al., 2013; Gibbon et al., 2000). Most large natural history museums of Colombia and Ecuador have divisions of herpetology. However, in most of these departments, the curator and main researchers are usually focused primarily on amphibians and reptiles therefore tend to be far less represented in general taxonomic production.

In general, effects of taxonomic uncertainty are higher at all analysis levels and for all studied groups, which is a constant issue with biodiversity data (Stribling et al., 2008). The unit of analysis of this study was species; however, different species concepts are applied by each zoological field for different taxa, thus they are not equivalent (Patten, 2015; Shanker et al., 2017; Zink, 2004). Subspecies are still widely used in Neotropical birds, but they are basically non-existent in Neotropical anurans or squamates, where the lowest taxonomic rank is species (Köhler et al., 2005; Phillimore and Owens, 2006). Current species and subspecies nomenclature in several clades of birds, anurans and squamates may not accurately reflect evolutionary diversity (Phillimore and Owens, 2006; Zink, 2004). Furthermore, in birds, there is a high level of taxonomic decisions that are made based on authority rather than evidence. There are several classification and rare-species committees that make decisions on the division and unification of species. They also make decisions related to the recognition of supra- and infra-species categories and validation of distribution records. However, in many cases, these committees often espouse both internally and externally dissonant views, and their methodologies do not always adhere to the norms of a peer-review system. A clear example of these practices and the uncertainties produced by them are the widely different lists of birds produced by the South American Classification Committee of the American Ornithological Society (Remsen et al., 2015) and the Handbook of the Birds of the World (del Hoyo et al., 2015; Tobias et al., 2010). Cryptic species may be prevalent in all studied groups and species currently conceived as widespread may be composite and include several undescribed taxa (Arteaga et al., 2016; Battey and Klicka, 2017;
Bickford et al., 2007; Giugliano et al., 2013; Murphy et al., 2016). In some groups, (especially in Brachycephaloidean anurans, Iguanian and Colubrid squamates and Tyrannid and Passerelid birds) the effect of taxonomic uncertainty biases diversity and endemicity analyses, thereby giving rise to incomplete maps of several areas. For example, the perceived low SR and endemicity in southern Ecuador (lowlands and highlands included) is caused by a lack of updated taxonomic data on *Pristimantis*, the most diverse vertebrate genus and member of the Brachycephaloidean-Terrarana clade. There are over 50 identified but still undescribed candidate species in southern Ecuador, many of which are probably endemic.

3.4.3 *Spatial biodiversity patterns: richness, endemicity and biogeographic regionalisation*

Plants, birds and mammals have historically been the main biogeographic model group in NWSA and analyses based on them have driven most biogeographic and conservation proposals. Many of these works were made possible by intensive efforts to create inventories of these groups, whose taxonomy and phylogeny are rather well-understood (Butchart and Bird, 2010; Schipper et al., 2008). Although Colombia and Ecuador are considered mega-diverse countries, information on the exact number and distribution of species in them is usually deficient and even conflictive. Even the number of birds, reptiles and amphibians species that occur in Colombia and Ecuador is uncertain, with different estimates varying among sources (‘AmphibiaWeb’, 2017; del Hoyo et al., 2015; Frost, 2015; Remsen et al., 2015; Ron et al., 2017; Torres-Carvajal et al., 2017; Uetz and Hošek, 2015). Reported differences are mainly due to data quality, periodicity and precision of data updating and taxonomic issues discussed in the previous section.

Data presented in this study shows that SR and endemicity of anuran, squamate and bird species are mainly concentrated in distinct areas that fully correspond with recognised biogeographic provinces but demonstrate
different and sometimes conflicting spatial patterns. It is unequivocal that, in general, the western Amazonia harbours the highest overall richness of terrestrial vertebrates (Bass et al., 2010). The western Amazonia in the Napo province exhibits the highest concentrated SR of amphibians. However, in reptiles and birds this pattern is less clustered, and while reptile and bird diversity is also concentrated in the wettest areas of Amazonia, they also occupy and are diversified in the drier areas. While all groups showed higher species richness in the Amazonian lowlands, it remains unclear if the heterogeneous patterns observed inside that region actually reflect real biogeographic patterns (i.e., riverine impact in birds, less aggregated distribution of species richness in reptile and more clustered in amphibians) or if they are caused by lower survey efforts in some areas of extreme eastern Ecuador, extreme north-eastern Peru and south-eastern Colombia. Lower regional SR in Amazonian towards Imeri and Sabana is most probably natural and related with lower precipitation and seasonality, similar to the trend observed between the Choco and drier areas of Guajira and in western Ecuador. Endemicity varies among clades, but I established that there was high endemicity in all study groups in the Andes mountain ranges. The complex geologic history and current topography of the Andes as well as its influence over the surrounding lands, are apparently one of the main promoters of the evolution of range-restricted species with small distributions areas (Arteaga et al., 2016; Duellman, 1988; Lynch and Duellman, 1997). However, this regional complexity is also affected by the ecological differences between the groups, with amphibians and reptiles having lower vagility and endemic species having very small ranges (and very high weighted endemism). Birds have higher vagility and endemic species with wider ranges.

The Northern Andes are herein recognised as part of the South American transition zone as a whole, including the Cauca and Paramo provinces, and not just the latter as Morrone claimed (2014a, 2017). Parsimony and UPGMA
analysis based on amphibians, reptiles and birds indicate that the Northern Andes is varied in its associations with provinces in the Pacific and Boreal Brazilian dominion. Cladistic biogeography analyses by Morrone (2014b, 2017, 2014a, 2005) and Urtubey et al. (2010) show the closed relationship between the Paramo, Desert and Puna with the Neotropical region. The status as a subregion comes from the three-distinct geographic and geologic units identified in the Andes (see Chapter 2): Northern Andes, Central Andes and Southern Andes. The Guajira province should herein be separated from the Sierra Nevada province based on its distinctive geologic, physiographic and biotic features. The Guajira provinces is thus defined as the coastal areas and lowlands of northern Colombia and extreme north-western Venezuela in the Maracaibo basin. The Sierra Nevada province is defined to be restricted to the slopes and highlands of the Sierra Nevada de Santa Marta mountain range. The Sabana province is herein considered as part of the Boreal Brazilian dominion, due to its close association with the Napo and Imeri provinces and according to parsimony analysis and UPGMA based on amphibian, reptile, and bird taxa presented herein.

Based on these data, I propose the following biogeographic hierarchical regionalisation of NWSA. Underlined regions are those to which I proposed biogeographic changes to Morrone’s proposals (Morrone, 2014a, 2017) based on parsimony and UPGMA analysis discussed above:

- Neotropical region Sclater, 1858
  - Brazilian subregion Schmarda, 1853
  - Pacific dominion
    - Guajira province Cabrera & Willink, 1973
    - Sierra Nevada province Müller, 1973, stat. nov.

17 See Appendix 1.
• Magdalena province Müller, 1973
• Chocó-Darien province Ryan, 1963
• Western Ecuador province Dinerstein et al. 1995\(^\text{18}\)
• Ecuadorian province Müller, 1973

- Boreal Brazilian dominion Clarke, 1892
- Sabana province Orfila, 1941
- Imerí province Beven et al., 1984
- Napo province Müller, 1973

- South Brazilian dominion Engler, 1882
- Yungas province Cabrera, 1971

• South American transition zone Morrone, 2004
  - Northern Andes subregion Udvardy, 1975, \textit{stat. nov.}
    - Cauca province Müller, 1973
    - Paramo province Cabrera, 1957

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\(^{18}\) Morrone (2014a) cited Morrone (1999) as author of the name of this region, however, Dinerstein et al. (1995) were the first authors to identify and name this region, using the name “Western Ecuador Moist Forest ecoregion”.
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Appendices

Appendix 1  New species of amphibians and reptiles discovered or described based on data analysed for this dissertation

1. *Rhaebo ecuadorensis* Mueses-Cisneros, Cisneros-Heredia, and McDiarmid, 2012 (Amphibia, family Bufonidae), previously confused with *Rhaebo glaberrhimus*, occurs in the Amazonia, from south-eastern Colombia, Ecuador, Peru, to central Brazil and north-eastern Bolivia at elevations between 215 and 1100 m (Mueses-Cisneros et al., 2012).


3. *Nymphargus orense* Cisneros-Heredia, Ron, Cogălniceanu & Székely, 2018 (Amphibia, family Centrolenidae), previously unknown but very similar to *Nymphargus grandisonae*.

4. *Centrolene* sp. 1 (Amphibia, family Centrolenidae), from the lowlands of southwestern Ecuador, previously confused with *Centrolene buckleyi*.

5. *Centrolene* sp. 2 (Amphibia, family Centrolenidae), from the lowlands of south-western Ecuador, previously confused with *Centrolene buckleyi*.

6. *Centrolene* sp. 3 (Amphibia, family Centrolenidae), from the eastern Andean slopes of Ecuador, previously unknown.

7. *Hyalinobatrachium* sp. (Amphibia, family Centrolenidae), from the Andean slopes of north-western Ecuador and south-western Colombia, previously confused with *Hyalinobatrachium valerioi* and *H. petersi*.

8. *Cochranella* sp. (Amphibia, family Centrolenidae), from the Andean slopes of south-eastern Ecuador and north-eastern Peru, previously confused with *Cochranella erminea*.

9. *Nymphargus* sp. (Amphibia, family Centrolenidae), from the Andean slopes of south-eastern Ecuador and north-eastern Peru, previously confused with *Nymphargus chancas*.

10. *Noblella* sp. 1 (Amphibia, family Craugastoridae), from the Andean slopes of north-western Ecuador, previously confused with *Noblella coloma*.

11. *Noblella* sp. 2 (Amphibia, family Craugastoridae), from the Andean slopes of south-eastern Ecuador, previously confused with *Noblella lochites*.

12. *Pristimantis* sp. 1 (Amphibia, family Craugastoridae), from the Andean slopes of eastern Ecuador, previously unknown.
13. *Pristimantis* sp. 2 (Amphibia, family Craugastoridae), from the Amazonian lowlands of Ecuador, previously unknown.

14. *Pristimantis* sp. 3 (Amphibia, family Craugastoridae), from the Amazonian lowlands of Ecuador, previously confused with *P. ockendeni*.


17. *Atractus esepe* Arteaga, Mebert, Valencia, Cisneros-Heredia, Peñafiel, Reyes-Puig, Vieira-Fernandes & Guayasamin, 2017 (Reptilia, family Colubridae), endemic to the Pacific lowlands of northern Ecuador at 100 m (Arteaga et al., 2017).


20. *Dipsas* sp. 1 Arteaga, Salazar-Valenzuela, Mebert, Peñafiel, Aguiar, Sánchez-Nivicela, Pyron, Colston, Colli, Cisneros-Heredia, Yáñez-Muñoz, Venegas, Guayasamin, Torres-Carvajal, 2018 (Reptilia, family Colubridae), endemic to the Pacific lowlands of southern Ecuador between 40 and 600 m.

21. *Sibynomorphus* sp. 1 Arteaga, Salazar-Valenzuela, Mebert, Peñafiel, Aguiar, Sánchez-Nivicela, Pyron, Colston, Colli, Cisneros-Heredia, Yáñez-Muñoz, Venegas, Guayasamin, Torres-Carvajal, 2018 (Reptilia, family Colubridae), endemic to the Pacific lowlands of western Ecuador between 5 and 300 m.

22. *Sibynomorphus* sp. 2 Arteaga, Salazar-Valenzuela, Mebert, Peñafiel, Aguiar, Sánchez-Nivicela, Pyron, Colston, Colli, Cisneros-Heredia, Yáñez-Muñoz, Venegas, Guayasamin, Torres-Carvajal, 2018 (Reptilia, family Colubridae), endemic to the Pacific lowlands of south-western Ecuador and north-western Peru between 40 and 1300 m.
Appendix 2 Species distribution reviews produced based on data analysed for this dissertation

11. *Hyalinobatrachium fleischmanni* (Amphibia: family Centrolenidae), geographic range expanded (Cruz et al., 2017).
12. *Pristimantis ockendeni* (Amphibia: family Craugastoridae), species excluded from the Northern Andes.
13. *Atractus microrhynchus* (Reptilia: family Colubridae), geographic range expanded (Passos et al., 2012).
14. *Atractus snethlageae* (Reptilia: family Colubridae), geographic range expanded (Schargel et al., 2013).
15. *Atractus major* (Reptilia: family Colubridae), geographic range expanded (Schargel et al., 2013).
Appendix 3 Spatial patterns of species richness of amphibians in north-western South America
Appendix 4

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

High : 118
Low : 1

0 500 km
Appendix 4 Spatial patterns of endemism of amphibians in north-western South America

Appendix 5a. Species richness of endemic amphibians to north-western South America

Appendix 5b. General spatial pattern of amphibian endemism index in north-western South America
Appendix 5a

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

0 500 km

Sources: Esri, USGS, NOAA

High : 57
Low : 1
Appendix 5b

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

High : 7.86776
Low : 8.04435e-008

0  500 km
Appendix 5 Spatial patterns of species richness of squamate reptiles in north-western South America
Appendix 6

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

High: 114
Low: 1

0 500 km
Appendix 6 Spatial patterns of endemism of squamate reptiles in north-western South America

Appendix 7a. Species richness of endemic reptiles to north-western South America

Appendix 7b. General spatial pattern of reptile endemism index in north-western South America
Appendix 7b

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

High : 0.56237
Low : 8.3438e-007

0 500 km
Appendix 7 Spatial patterns of species richness of birds in north-western South America
Appendix 8

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

High : 520
Low : 1

0  500 km
Appendix 8 Spatial patterns of endemism of birds in north-western South America

Appendix 11a. Species richness of endemic birds to north-western South America

Appendix 11b. General spatial pattern of bird endemism index in north-western South America
Appendix 9a

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

High: 58
Low: 1
Appendix 9b

Coordinate System: GCS WGS 1984
Datum: WGS 1984
Units: Degree

High : 11,0001
Low : 1,36839e-009

0  500 km
## Appendix 9 Data matrix of species and biogeographic provinces

Data matrix of species and biogeographic provinces used for biogeographic analyses, in comma-separated-values format. Presence is marked as 1 and absence as 0. The following order of records is followed for the biogeographic provinces: Choco, Ecuadorian, Guajira, Imeri, Magdalena, Northern Andes, Napo, Sabana, Santa Marta, Western Ecuador, Yungas.

<table>
<thead>
<tr>
<th>Species</th>
<th>Choco</th>
<th>Ecuadorian</th>
<th>Guajira</th>
<th>Imeri</th>
<th>Magdalena</th>
<th>Northern Andes</th>
<th>Napo</th>
<th>Sabana</th>
<th>Santa Marta</th>
<th>Western Ecuador</th>
<th>Yungas</th>
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For the sake of completeness, the full list of species and their corresponding presence (1) or absence (0) of specific traits is provided. The table includes a variety of snakes from different genera, each with a profile of traits or characteristics. This format allows easy identification and comparison of species in a structured manner.
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Drymobius rhombifer,1,1,1,1,1,1,1,1,1,1,0
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Echinosaura horrida,1,1,0,0,0,1,0,0,0,1,0
Echinosaura orcesi,1,0,0,0,0,1,0,0,0,0,0
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Emmochliophis miops,1,0,0,0,0,1,0,0,0,0,0
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Helicops petersi,0,0,0,0,1,1,0,0,0,0,0
Helicops polylepis,0,0,0,1,0,1,0,0,0,0,0
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Chapter 4  Systematic literature review and evidence synthesis of impacts of habitat change on amphibians, reptiles and birds of the tropical Andes
4.1 Introduction

Over the past two centuries, humans have become a global force able to change natural ecosystems at rates previously unseen (Hassan et al., 2005; Secretariat CBD, 2006, 2010a, 2014). Human-driven habitat change, including land use and land cover modifications, has been identified as the anthropogenic action having the most widespread, intense, and extensive impacts on biodiversity (Andrén, 1994; Saunders et al., 1991; Secretariat CBD, 2010b, 2010b; Hassan et al., 2005; Secretariat CBD, 2014). Decline and extinction events produced by habitat change jeopardize the long-term survival of species, biological communities, and ecosystems (Ehrlich and Ehrlich, 1992; Foley et al., 2005; Mace et al., 2005; Secretariat CBD, 2010b; Hassan et al., 2005). Human-driven habitat change rates are accelerating globally due the needs of more than seven billion people. While Earth’s natural resources are increasingly diverted toward human use and consumption, human-driven habitat change undermines the capacity of ecosystems provide the natural resources and ecosystem services at local, regional, and global levels necessary to sustainability (Foley et al., 2005; Mace et al., 2012; UN, 2017; Secretariat CBD, 2014).

In 2002, at the Convention of Biological Diversity (CBD), world leaders agreed to significantly reduce the rate of biodiversity loss by 2010. This target was established alongside goals of poverty alleviation and to the benefit of life on the planet (Mace and Baillie, 2007; Secretariat CBD, 2005). The biodiversity target was also incorporated into the United Nations’ Millennium Development Goals – Goal 7: “Ensure environmental sustainability”—with special emphasis on reversing the loss of environmental resources and biodiversity (UN, 2017, 2000). However, by 2010, the goal was achieved neither globally nor regionally, with many species still sharply declining as
much in abundance as in distribution. The number of species at risk of extinction keeps increasing and many biodiversity-sensitive regions continue to decline. Most indicators show no significant improvement nor trend reversal of the global status of biodiversity. Most indicators show negative trends and pressure indicators point out that trends have kept rising over recent decades. There is undeniable evidence that the 2010 UN target was not met.

However, the significance of several indicators of the evaluation of the 2010 7th Millennium Goal was found heterogeneous. Most had grave gaps in terms of geographic, temporal or taxonomic coverages. Information on the trends of habitat change was incomplete, with large groups of organisms (including large clades of plants, vertebrates, and invertebrates) not included in evaluations of the status of threatened species. Trends of abundance and distribution lacked for most species. Significant data was missing for time periods, i.e. before 1980 and after 2005 (Balmford et al., 2005; Butchart et al., 2010; Walpole et al., 2009; Secretariat CBD, 2006, 2010a).

Following these mixed results, the Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets were established as a ten-year framework for action to save biodiversity and enhance its benefits for people (Secretariat CBD, 2010b). The Aichi targets focused on five strategic goals: (a) Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society; (b) reduce the direct pressures on biodiversity and promote sustainable use; (c) improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity; (d) enhance the benefits of all from biodiversity and ecosystem services; and, (e) enhance implementation through participatory planning knowledge management and capacity building (Secretariat CBD, 2010b). Human-driven habitat change is a
transversal issue to all these strategic goals. Causes that imperil biodiversity and their respective degree of impact are key factors for the development of conservation action plans. However, management measures are frequently implemented only considering few groups of species.

In order to understand the status of knowledge about the impacts of habitat change on the vertebrate diversity of north-western South America, I conducted a systematic review of the literature regarding impacts of habitat change on amphibians, reptiles and birds of the tropical Andes and I developed an evidence synthesis of the identified data.

4.2 Methodology

4.2.1 Methodological approach

This chapter aims to exhaustively identify, report and synthesise evidence-based research regarding the impacts of habitat change on three clades of terrestrial vertebrates in the Neotropical region. To achieve this aim, I conducted a systematic literature review (SLR). A SLR is a process that aims to answer a given research question by identifying all relevant sources through an exhaustive and comprehensive search. The SLR process includes the appraising of all evidence with a qualitative assessment and the presentation of results in a critical and narrative synthesis, accompanied with a tabular summary of all identified citations. Such an approach allows the analysis of what is known and remains unknown and ultimately provides recommendations for future research (Grant and Booth, 2009; Higgins and Green, 2011). This SLR’s evidence synthesis was performed narratively as a meta-analysis was not deemed feasible due to data heterogeneity (Dixon-Woods et al., 2005; Rodgers et al., 2009).
4.2.2 Study question and search strategy

In this review, the concept of habitat change loosely comprehends all human-driven habitat changes. The study question focuses on vertebrate animals, and more specifically on the taxa of the following clades: Amphibia, Reptilia, and Aves. While there are many ways of reporting impacts, I chose to limit reporting to academic (= peer-reviewed) literature. The PICOS framework (Population, Intervention, Comparison, Outcomes, and Study Types,
Table 1) was used to define the study question (Higgins and Green, 2011).
Table 1  
**PICOS framework used to define the research question**

<table>
<thead>
<tr>
<th>Item</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Population</strong></td>
<td>Vertebrates, exclusively amphibians, reptiles, and birds</td>
</tr>
<tr>
<td><strong>Interventions</strong></td>
<td>Habitat change, including all types of land use and land cover modifications</td>
</tr>
<tr>
<td><strong>Comparators</strong></td>
<td>Not applicable</td>
</tr>
<tr>
<td><strong>Outcomes</strong></td>
<td>Any impact</td>
</tr>
<tr>
<td><strong>Study Type</strong></td>
<td>Academic literature, primary and secondary bibliography, including observational and natural history studies, prospective ecological studies, interventional studies, and all types of reviews</td>
</tr>
</tbody>
</table>

Searches were conducted on Scopus® using the database native search engine. Scopus is the largest abstract and citation database of peer-reviewed literature, with more than 69 million records dating back as far as 1788, and references included on records back as far as 1970. Scopus is developed by Elsevier and is accessible by subscription. Scopus coverage focuses on primary literature from the following main source types: serial publications published with an International Standard Serial Number ISSN (e.g., journals, book series and conference series) and, non-serial publications published with an International Standard Book Number ISBN, such as one-off book publications or one-off conferences. Scopus coverage is global, with titles from all geographic regions, including more than 700 titles published in Latin America, and with over 20% of titles published in languages other than English (Burnham, 2006; Elsevier, 2017).

The search strategy was adapted to Scopus search engine configurations and focused on titles and abstracts. Search terms were broad to allow an inclusive selection of citations. Boolean terms served as connectors. To be as inclusive as possible, search terms included all major taxonomic categories and
common names (Appendix 1). A set of known relevant citations served as validation to the search strategy.

4.2.3 Screening, data extraction and evidence synthesis

Citations identified by the Scopus search were reviewed at two subsequent stages. First, titles and abstracts of all citations were reviewed based on a set of eligibility criteria.
Table 2). Retained citation were then full-text reviewed based on the same set of eligibility criteria. Upon completion of the reviewing process, a PRISMA flow diagram reporting the process was developed (Moher et al., 2009).
### Table 2  Eligibility criteria

<table>
<thead>
<tr>
<th>Category</th>
<th>Exclusion criteria</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>0. Null entries, duplicates, not in the language of interest, abstract is reported elsewhere and not in the time period of interest</td>
<td>01 - Null entries</td>
<td>No information is reported in title and abstract fields.</td>
</tr>
<tr>
<td></td>
<td>02 - Duplicates</td>
<td>Duplicate of an existing entry</td>
</tr>
<tr>
<td></td>
<td>03 - Not in the language of interest</td>
<td>Documents in languages other than English, Spanish, Portuguese or French</td>
</tr>
<tr>
<td></td>
<td>03 - Abstract that is reported elsewhere</td>
<td>Abstracts and contents that have been reported in another publication</td>
</tr>
<tr>
<td>1 - Nature of study</td>
<td>10 - Not the study type of interest</td>
<td></td>
</tr>
<tr>
<td>2 - Population</td>
<td>20 - Not animal</td>
<td>Focusing on plants, fungi, unicellular or other groups of biodiversity but not on animals</td>
</tr>
<tr>
<td></td>
<td>21 - Not vertebrate animal</td>
<td>Focusing on invertebrates, not on vertebrates</td>
</tr>
<tr>
<td></td>
<td>22 - Not focus clades</td>
<td>Focusing on mammals or fishes</td>
</tr>
<tr>
<td></td>
<td>23 - Not Neotropical</td>
<td>From the Old World, Neartic, Chile or Patagonia</td>
</tr>
<tr>
<td></td>
<td>24 - Not tropical Andes</td>
<td>From countries other than Venezuela, Colombia, Ecuador, Peru or Bolivia</td>
</tr>
<tr>
<td></td>
<td>25 - Not NW South America</td>
<td>Not from mainland Venezuela, Colombia, Ecuador, and NW Peru</td>
</tr>
<tr>
<td>3 - Outcome</td>
<td>30 – Not including any impact</td>
<td>The endpoints of interest are: impacts by habitat and land use change</td>
</tr>
<tr>
<td>4 - Potential</td>
<td>40 - Potential</td>
<td>Citation with eligible population, study type and outcomes</td>
</tr>
<tr>
<td>5 - Cannot decide</td>
<td>51 - Cannot decide</td>
<td>Title and abstract do not provide enough information for a decision</td>
</tr>
</tbody>
</table>
All publications were accessed online, either through their open access portals, using academic access (Shibboleth) or by looking for full-text using Google search engine. All citations retained after full-text review were included as part of the systematic review. All relevant evidence to the study question were extracted onto an Excel worksheet, including the following data: study type, dates, country, locality, elevation, taxa, objectives, methods, impact type, habitat change type, and outputs.

4.3 Results

4.3.1 Overview

Searches were conducted on 06 December 2016 and 4098 citations were identified through database searching. After screening of title and abstracts, 246 citations were selected, and 3852 were discarded as did not meet inclusion criteria. After assessing eligibility by full-text review, 84 citations, associated with 74 studies, were identified and included in the narrative synthesis, and 162 were discarded (Appendix). In total, 4014 citations were excluded (Figure 1).

\footnote{Some retained publications had the same data obtained from a single study but analysed under research questions of perspectives. They are counted as different citations of one study.}
Figure 10  PRISMA flow diagram
4.3.2 Study characteristics

A majority of the 82 publications included in this review reported observational studies (91%). Other types of studies or studies with a combination of different types were represented by few publications (exploratory studies, model-based studies, review studies).

![Graph showing types of studies and number of publications](image)

**Figure 11** Types of studies and number of publications included in this review on impacts of habitat change of amphibians, reptiles and birds of north-western South America

The oldest identified study was published in 1994 (Figure 12). Most studies were published recently, with 49 studies since 2010 (Appendix 2). Almost all studies involved only one or two-year periods of field data collection, which in most cases corresponded to only a few months of effective work. Most studies did not explicitly report the sampling effort. Only two studies involved field data collected over more than 10 years (Aguilar et al., 2016; Feeley and Terborgh, 2008), and four studies included field data collected over 6–8 years (Cole et al., 2014; Kattan et al., 2006; Lynch, 2015; Marín-Gómez et al., 2016). Interestingly, two of the broadest timeframe studies are based on
natural history data, collected by casual observations and collections (Aguilar et al., 2016; Lynch, 2015).
Studies published between 1994 and 2009, showing the duration of field data collection (in years)
Figure 12  Studies published between 2010 and 2016, showing the duration of field data collection (in years) (continued)
This review shows that the geopolitical and geographic distribution of studies is unequal. Most studies were done in localities in Colombia (59%), followed by Ecuador (32%) (Figure 13). Two studies were conducted in several localities of Venezuela, Colombia and Ecuador, and one study at localities of all north-western South America, from Venezuela to Peru. Most studies were conducted in the High Andes of north-western South America, with particular emphasis on the slopes and highlands of the Cordillera Occidental of the Andes of Colombia and Ecuador, and on the slopes and highlands of Cordillera Central and Cordillera Real of Colombia and Ecuador. A significant portion of studies was conducted on the Amazonian and Orinoquian lowlands. Few studies were conducted in the Pacific lowlands, Cordillera Oriental of Colombia, Cordillera de Merida of Venezuela or Sierra Nevada de Santa Marta.

Figure 13. Number of studies according to countries
Figure 14. Number of studies according to physiographic regions and subregions of north-western South America.

Elevational data was reported in 62 studies. Most research on the impact of habitat change was focused on the slopes of the Andes, between 1000 and 3000 m elevation, followed by the lowlands (< 1000 m elevation, 26 studies). Only six studies were reportedly done at higher elevations (> 3000 m).

Most studies were focused in birds (65%), with only 20 studies dealing with amphibians (24%) and 8 studies with reptiles (10%). One studies used combined data from all three groups. Most studies dealt with entire communities, but 11 studies dealt with single species, two at taxonomic family-level, four with specific faunal assemblages, and two with migratory birds.
Research was mainly focus of impacts caused by agricultural expansion (82%), followed by infrastructure development (21%), urban expansion (9%) and impacts of tourism on habitat (1%).

Basically, all studies have been conducted using only one monitoring or evaluation method, the most common being visual transects and visual count-points. Nine studies used mist-netting for bird surveys, while 20 studies mixed visual transects with audio recording for calls. Other less common methods included: Distribution modelling (two studies), analysis of compiled databases, radio transmission, and artificial bird nest (one study each).

Most studies (51%) reported negative impacts produced by human-driven habitat change in amphibians, reptiles and birds. Negative impacts affected mainly the distribution and composition of animal communities, but also the population or the ecological adaptations of species. Some studies (24%) reported beneficial impacts caused by habitat change, the most common related with increase of species richness and abundance, but also with expansion of the distribution range, increase in population, or morphological changes. Mixed effects were reported in 22% of the publications.

4.3.3 Evidence synthesis

In this section, the main results and conclusions of each publication will be synthesised.

Researchers have used different methodologies to assess amphibian richness and results showed significant variations across methods (Whitworth et al., 2017). Due to the difference in those results, researchers recommended the use of appropriate tools that better adjust to the requirements of the study (Whitworth et al., 2017). In Ecuador researchers evaluated how Lidar and optical texture models can predict bird diversity, thereby establishing that
both methodologies do not provide significantly different result (Wallis et al., 2016). Optical texture metrics is appropriate to predict the Shannon index but has limitations when describing phylodiversity (Wallis et al., 2016).

Alongside the development of a natural gas exploration platform in the Peruvian region of Madre de Dios, researchers used acoustic monitoring tools to evaluate the effect of such infrastructure over anuran and bird populations (Deichmann et al., 2017). While the richness of anurans increased with proximity to the platform, bird richness seemed to decrease (Deichmann et al., 2017). While nectarivorous birds were more frequently detected during the drilling phase, insectivorous bird richness decreased with proximity to the platform (Deichmann et al., 2017). In the process of assessing the effects of petroleum extraction in the Ecuadorian Amazon, researchers found that insectivores bird abundance decreased with proximity to the platform, while other birds did not show significant differences across the gradient of disturbance (Canaday and Rivadeneyra, 2001).

Researchers in Colombia have compared carbon measurements and amphibian richness in a secondary forest in process of restoration. They found that as the forest matures, species richness increases (Basham et al., 2016). With maturity, the composition of the community gets more similar to a primary forest, including the presence of red-listed species (Basham et al., 2016). Carbon stocks and the richness of amphibian species seem to be positively related (Basham et al., 2016).

In the Amazonian region of Colombia and Brazil, researches have studied how social and economic factors influence environmental profiles of farms over a deforested region (Lavelle et al., 2016). They found that the agroforestry seems to be the production method where production was the highest and the
effect on biodiversity was the lowest effect (Lavelle et al., 2016). Researchers suggest that agroforestry and silvopastoral production have promising results for the increase of production and sustainability (Lavelle et al., 2016). In Colombia researchers evaluated patterns of change in body condition of migratory birds in order to evaluate the sustainability of shaded plantations for overwintering, four of the eight birds analyzed showed an increase in body condition throughout the day (Colorado Zuluaga and Rodewald, 2017).

The patterns of distribution of raptors is been affected by deforestation. An increase in deforestation may lead to severe reductions in raptor populations across the Andes (Thiollay, 1996). In the western Andes of Colombia deforestation is a concern as bird species have smaller distribution ranges than the ones living in forested zones (Ocampo-Peñuela and Pimm, 2015). Trends in variation of effects of deforestation over populations change over trophic levels (Ocampo-Peñuela and Pimm, 2015).

Researchers in Peru have compared avian richness between a forest and a palm oil plantation finding that in the forest the avian richness was significantly higher (Srinivas and Koh, 2016). The community was significantly different in both landscapes, with just 5% of species being common to both areas (Srinivas and Koh, 2016). The results of this research suggest that oil palm plantations are very poor habitats for avian life in the amazon forest (Srinivas and Koh, 2016). In Colombia researchers assessed the impacts of oil palm plantations on bird populations, finding that functional diversity was significantly higher in remnant forest (Prescott et al., 2016b). In pastures and oil palm plantations, levels of species richness were strongly associated with the proximity of remnant forest (Prescott et al., 2016b). Terrestrial foraging and aquatic birds were mostly associated with pastures, while frugivorous and canopy foraging birds were associated with remnant
forest (Prescott et al., 2016b). In Colombia researchers studied the effects of oil palm agricultural expansion on the phylogenetic diversity of birds and found that diversity was significantly higher in forests than in oil palm plantations, but no significant differences were identified between pastures and plantations (Prescott et al., 2016a). Researchers recommend the development of palm oil plantations over pastures rather than over forests (Prescott et al., 2016a). African palm plantations are a concern for snake conservation, due to the loss of habitat that this represents (Lynch, 2015). The community composition of environments altered by African palm plantations tend to be more homogenous with high dominance of few species (Lynch, 2015). In landscapes where there is disturbance associated with oil palm plantations, the probability of occupancy of birds increase with the availability of nearby forest remnants (Gilroy et al., 2015). However, the occurrence of reptiles and amphibians is not predicted by proximal forest remnants (Gilroy et al., 2015).

Researchers in Colombia have evaluated the prevalence of haematosporidian parasites in endemic bird areas. They found that 31% of surveyed birds were infected with at least one haematosporidians genera (Gonzalez-Quevedo et al., 2016). Prevalence of infection inversely associated with altitudes (Gonzalez-Quevedo et al., 2016). Endemic birds seem to have higher infection rates than the non-endemic ones (Gonzalez-Quevedo et al., 2016).

Using passive acoustic monitoring, researchers in Peru measured avian and amphibian richness in a forest and an active gold mine. They found that bird richness did not differ between both habitats (Alvarez-Berríos et al., 2016). However, bird communities change due to human activities along time., and the richness of sensitive birds was significantly lower in the mine than in the forest (Alvarez-Berríos et al., 2016). However, anuran richness was lower in the forest than in the disturbed area (Alvarez-Berríos et al., 2016).
To understand the factors contributing to the decrease of amphibians in human-disturbed areas, researchers in Colombia evaluated the turnover of anurans between altered zones and natural vegetation types. They found that the highest turnover was between forested and human-altered areas (Méndez-Narváez and Bolívar-G, 2016). Fine scale analysis showed that the most important factor for anuran decreases was the loss of microhabitats (Méndez-Narváez and Bolívar-G, 2016). Species seem to have more niche overlap in human-altered areas than in pristine ones (Méndez-Narváez and Bolívar-G, 2016).

Researchers in Peru studied the differences between terra firme and floodplain in amazon rainforest for avian communities. They found significant differences in bird families and reproductive characteristics (Lieshout et al., 2016). In Esmeraldas, in coastal Ecuador, it is reported that waterbirds use shrimp ponds in order to get food (Cheek, 2009).

In Armenia, Colombia there are reports of threatened birds using urban landscapes as a response of habitat loss (Martínez and Serrano-Cardozo, 2017). *Dacnis hartlaubi* and *Setophaga cerulea* use urban settings as a passage and wintering area (Martínez and Serrano-Cardozo, 2017). In Ecuador, *Mimus gilvus* is rapidly colonizing new environments, possibly because of the facilitation provided by the change of land use (Aguilar et al., 2016). Caprimulgidae birds have been reported to use human provided structures to successfully colonize disturbed habitats (Ingels et al., 1999).

An assessment on the current distribution of *Automolus rufipectus* reflects that almost half of the total population lives in a protected area (Botero-Delgadillo et al., 2015). Compared to previous research, it seems that the geographical...
and altitudinal distribution of this species is increasingly restricted (Botero-Delgadillo et al., 2015).

A study of the abundance responses of 43 amphibian and 61 reptile species in several countries of Latin America reported that 90% of reptiles and 96% of amphibians are showing edge responses (Schneider-Maunoury et al., 2016). The abundance of almost three quarters of amphibians and over the half of reptiles is decreasing with proximity of the forest edge (Schneider-Maunoury et al., 2016). There are few species in which the edge effect is opposite (Schneider-Maunoury et al., 2016). In the North-Western Biosphere Reserve in Peru, bird diversity seems to be higher in the forest edge and the buffer zone than in the forest interior (Piana and Marsden, 2012). In places where human intervention is different, anuran assemblages differ in composition (Burbano-Yandi et al., 2015). In a village landscape dominance tend to be higher and diversity lower in comparison to an intervened forest (Burbano-Yandi et al., 2015). Several species were exclusive of one of those environments (Burbano-Yandi et al., 2015). Comparing the community assemblages of birds in secondary forests and Andean alder stands, researchers found that at least 27 species were exclusive of the Andean alder stand (Castaño-Villa, Estevez, et al., 2014). There were low similarities in community composition. However, bird richness and abundance did not differ significantly (Castaño-Villa, Estevez, et al., 2014). In Ecuador, researchers tried to evaluate the populations dynamics of *Pristimantis* frogs in the Andes and reported annual variations in sex and species composition (Cole et al., 2014). During the course of the study *Pristimantis bicantus* had significant reductions in populations (Cole et al., 2014). Amphibian richness and diversity change across a gradient of human disturbance (Oldekoop et al., 2012).
Researchers in the northern Andes studied how bird communities vary according to land use changes, concluding that bird richness is more positively associated with silvopastoral landscapes than coffee plantations (Colorado Zuluaga and Rodewald, 2017). Insectivores species were associated with secondary forest (Colorado Zuluaga and Rodewald, 2017). Researchers in Colombia assessed the efficacy of agroforestry systems to preserve bird biodiversity. In both analysed agroforestry systems, the increase in tree coverage was related with an increase in human activity (McDermott et al., 2015). Abundance of migratory birds in those landscapes was positively related with the structural complexity of the plantation (McDermott et al., 2015). Researchers in the Ecuadorian Andes determined that bird richness was related to floristic composition of the habitat (Tinoco et al., 2013). Connectivity of forest patches contributed to the abundance of generalist bird species (Tinoco et al., 2013).

In the evaluation of the effect of altitudinal variation in bird response to human disturbance, it seems that species richness declines with altitude and disturbance (Villegas and Garitano-Zavala, 2010). Open fields tend to have a higher reduction in species richness (Villegas and Garitano-Zavala, 2010). *Eriocnemi nigrivestis* populations have been analysed in the slopes of the Pichincha volcano in Ecuador. Although this species seems to be resistant to microhabitat alterations, the poor connectivity of populations was identified as a severe threat for survival (Guevara et al., 2015).

In Colombia, researchers have evaluated the benefits of strategic management of croplands over phylogenetic diversity of birds. Their results show that land-sharing practices have positive results over bird diversity (Edwards et al., 2015). Even effects of cattle settlements can be avoided by a correct land-share (Edwards et al., 2015).
In a study of a bird community in Colombia, researchers identified that tree basal area, stem diameter, and number of stems were characteristics related with the increase of diversity and abundance (Castaño-Villa, Ramos-Valencia, et al., 2014). However, in this study authors did not find linear relationships between the mentioned characteristics and abundance nor richness (Castaño-Villa, Ramos-Valencia, et al., 2014). Heterogeneity in basal area was highly correlated with an increase in richness and abundance of insectivorous birds (Castaño-Villa, Ramos-Valencia, et al., 2014). In the Cuyabeno Reserve, Ecuador, researchers found that the presence of insectivorous birds was highly correlated with the absence of human impact (Canaday, 1996). Understory insectivorous birds and canopy frugivores were found to be more vulnerable to extinction (Kattan et al., 1994). In Bolivia, researchers determined that forest disturbance effects were higher in bird species that are specialist of the humid forest (Aben et al., 2008). Insectivorous birds abruptly decreased in abundance with disturbance (Aben et al., 2008). The effects of habitat reduction over bird populations seems to be a bottom-up process in the case of insectivorous species (Feeley and Terborgh, 2008). On islands of forest with mammal species inhabiting there, bird populations decrease was reduced (Feeley and Terborgh, 2008).

In Bolivia, researchers have found that frugivorous bird diversity is higher in the forest edges, where the is more fruit availability (Saavedra et al., 2014). Functional and interactional evenness did not differ in the forest interior and edges. However functional and interactional diversity were higher in the edges than in the forest interior (Saavedra et al., 2014).

Species response to edge effect are mostly guided by taxon, understory bird and amphibian richness decreases with proximity to a road in Ecuador (Whitworth et al., 2015). However, some birds, especially diurnal ones,
increase with proximity to the road (Whitworth et al., 2015). From an overall perspective diversity reduces by 32% with the presence of a road (Whitworth et al., 2015). The edge effect of pasture systems over reptiles seems to differ between dry and rainy seasons. Most of the factors contributing to the accentuation of the edge effect are microhabitat characteristics (Carvajal-Cogollo and Urbina-Cardona, 2015). Researchers in a lowland Amazonian rainforest in Ecuador have evaluated the road-edge effects over amphibian and reptile populations and found that habitat characteristics highly differ due to the edge effect of the road; an effect that extend up to 100m from the road (Maynard et al., 2016). Amphibian and reptile abundance and diversity were lower in the edge area than in the interior forest (Maynard et al., 2016). Vine abundance was a great predictor of amphibian abundance, while diversity was well predicted by both vine and mature tree abundance (Maynard et al., 2016). Analysing vertebrate mortality in a road in Venezuela, it was determined that reptiles are the most vulnerable group (Seijas et al., 2013). Relative collisions have increased in relation to data from twenty years ago due to the increase in traffic and changes in land use (Seijas et al., 2013). In the Cauca valley, Colombia, researcher have determined that amphibians and reptiles are most vulnerable to road mortality (Vargas-Salinas et al., 2011). Amphibians were the taxa most affected by the presence of a road and diversity increased with distance from a road (Vargas-Salinas et al., 2011). However, some species of amphibians and reptiles were exclusively inhabiting near road landscapes (Vargas-Salinas et al., 2011). In Ecuador, researchers measured the occupancy of bromelains in the canopy of a forest with an oil road and in undisturbed forest, they found that in the undisturbed forest, there was higher abundance and occupancy (McCracken and Forstner, 2014). This result suggests that minimal footprint can have repercussions on the amphibian community in pristine forests (McCracken and Forstner, 2014).
In Colombia researchers compared bird abundance and richness between alder plantations and secondary forest. They found that habitats are not equivalent (Salazar-Ramírez et al., 2014). At the alder plantation, diversity and abundance of nectarivorous and frugivorous birds was higher (Salazar-Ramírez et al., 2014).

In the Choco region, in the Pacific lowlands of Colombia and Ecuador, researchers evaluated how farmland serves as adequate habitat for birdlife. They found this to be highly context-dependent (Gilroy et al., 2014). Occurrence of bird species was related with proximity to forest remnants and small-scale wildlife-friendly habitats (Gilroy et al., 2014). Bird diversity and abundance was constant over landscapes (Gilroy et al., 2014).

By doing hierarchy models of species occupancy, researchers determined that palm plantations have higher species diversity than cattle farms (Gilroy et al., 2015). For bird communities the presence of forest remnants in a 250m radius significantly increased the possibility of occupancy in the palm plantation. However, this phenomenon did not occur for amphibians or reptiles (Gilroy et al., 2015).

In Colombia, researches have compared avian response to cattle pasture in relationship with forest. Their results show that open field species abundance increased in cattle pastures (Gilroy et al., 2015). Cattle grazing landscapes in Colombia seem to have heterogeneous bird communities, as a result of proximity to riparian habitats (Elías Domínguez-López and Ortega-Álvarez, 2014). Due to the simple structure of the landscape, crop fields tend to have poor diversity (Elías Domínguez-López and Ortega-Álvarez, 2014).

In a study carried out in Colombia, different vegetation structured landscapes were predictors of amphibian occupancy and abundance (Cortés-Gómez et al., 2013). The most critical factor for predicting amphibian abundance was canopy cover (Cortés-Gómez et al., 2013). The necessary habitat for the
presence of healthy amphibian communities was over three quarters of canopy coverage and a high density of woody plants (Cortés-Gómez et al., 2013).

In Ecuador, researchers have determined that bird richness increases with disturbance but decrease with habitat loss (Durães et al., 2013). In fragments of endemic forest, threatened birds decrease by three quarters in comparison to continuous forest (Durães et al., 2013). Habitat loss was a predictor of decreased bird populations, with a high dominance of a few generalist species (Durães et al., 2013). In gallery forest fragments bird diversity seems to be higher than in tree islands (Muñoz et al., 2013). Savanna rangeland that surrounds forest islands is acting as a filter that merges bird abundance (Muñoz et al., 2013). Connectivity of forest fragments is necessary for the conservation of bird species with low niche plasticity (Muñoz et al., 2013). In Peruvian Amazon bird diversity does not seems to be dependent on bamboo forest (Socolar et al., 2013). In Colombia, researchers have evaluated fluctuation of feather asymmetry as a consequence of forest fragmentation: in the most fragmented forests, asymmetry was higher (Cuervo and Restrepo, 2007). With this study there was no confirmed pattern of fluctuating asymmetry in feathers (Cuervo and Restrepo, 2007).

In an abandoned pasture in Bellavista, Ecuador, bird richness was found to increase each year. However, during the conduct of this study, the pasture did not present the same amount of species recorded in undisturbed forest (Welford, 2000). Abandoned pastures increase the probability to host migratory birds with the years after being abandoned (Andrade and Rubio-Torgler, 1994). In the Yachana Reserve, Ecuador, researchers determined that reptile and amphibian diversity and abundance was lower in plantations and pasture habitats (Beirne et al., 2013). Abandoned pastures landscapes showed
high abundance of herpetofauna but low diversity and richness (Beirne et al., 2013). Abandoned plantation sites showed high diversity and richness but with low relative abundance (Beirne et al., 2013).

As in the forest, anurans form assemblages in disturbed areas, these assemblages are characterized by having a different composition than the ones in the forest (Cáceres-Andrade and Urbina-Cardona, 2009). In Mache Chindul reserve, Ecuador, researchers found an inverse correlation between human intervention and amphibian richness in rivers (Jongsma et al., 2014). Amphibian assemblages differ in composition according to human disturbance (Jongsma et al., 2014). Amphibian diversity and species richness were higher in primary forests than in secondary ones (Jongsma et al., 2014).

In Machalilla National Park, Ecuador, researchers evaluated the richness of birds in habitats with different levels of disturbance. They identified a variation in the dry forest between more and less disturbed sites. In arid scripts, no such species richness was identified (Knowlton and Graham, 2011).

In a study carried out in the Serrania de los Paraguas, in Colombia, researchers reported that amphibian richness was higher in the forest than in pastures (Isaacs Cubides and Urbina-Cardona, 2011). Community composition differ from pastures and forests, with some species, exclusively inhabiting forests (Isaacs Cubides and Urbina-Cardona, 2011). In Colombia, researchers have studied the microhabitats of Geobatrachus walkeri (Anura: Strabomantidae) and reported that the majority of individuals were found in pine plantations (Martínez Baños et al., 2011).

Research in the Colombian Andes shows that birds use live fences for several purposes, including connectivity. Live fences could be used by birds even in
environments that have major disturbance and alterations (Pulido-Santacruz & Renjifo, 2011).

A review, carried out over the adaptation of birds to agricultural systems in Latin America, found that about 87% of migratory birds occur in agroecosystems (Díaz-Bohórquez et al., 2014). Structural complexity and tree coverage increase the chance of migratory birds occurring those systems (Díaz-Bohórquez et al., 2014). Rice plantations serve as a refuge for migratory aquatic birds (Díaz-Bohórquez et al., 2014). In the savanna of Bogota, in Colombia, researchers analysed the density and abundance of aquatic birds, reporting that the availability of wetlands is the main factor to predict aquatic bird occupancy (Rosselli and Stiles, 2012). Coot and gallinula abundance is negatively related with urban habitats. However, researchers suggest that urban wetlands are very important for the conservation of other aquatic birds (Rosselli and Stiles, 2012). In an altered environment, migration can present difficulties. Researchers in Colombia followed the trajectory of several migratory birds in order to identify how are they adapting to habitat changes (Suarez-Rubio et al., 2015). Swainson's Thrush did not present difficulties to cross over disturbed areas, while understory resident species seem to avoid such zones (Suarez-Rubio et al., 2015). Researchers in Colombia have studied the effect of agroforestry landscapes over a migrant bird community and have found that species richness is mainly associated with habitat characteristics (Colorado Zuluaga et al., 2016). Those characteristics are related with the availability of giving the birds diversity of food resources (Colorado Zuluaga et al., 2016). Results of this research suggest that birds can be beneficiated from the structural management of agroforestry and silvopastoral systems (Colorado Zuluaga et al., 2016). Researchers in Colombia evaluated the efficiency of silvopastoral systems in the conservation of neotropical migrant
birds, founding that the complexity of the system is positive related with a higher diversity (McDermott and Rodewald, 2014). *Setophaga fusca* was more commonly detected in other habitats than in silvopastoral systems, possibly because this bird prefers more complex systems (McDermott and Rodewald, 2014). In Bogota, Colombia, researchers have evaluated the risk of collision of birds to windows and determined that windows in which birds can see vegetation on the other side are more dangerous than the ones that do not (Agudelo-Álvarez et al., 2010). Window collision seems to be a threat to boreal migrant species (Agudelo-Álvarez et al., 2010). Migratory cerulean warbler (*Dendroica cerulea*) in Venezuela is seen using coffee shade plantations with high site fidelity (Cruz-Delgado et al., 2010).

In Ecuadorian Andes, bird community composition is strongly associated with canopy coverage (Mordecai et al., 2009). In the driest season, birds stopped using the most disturbed areas (Mordecai et al., 2009). In Colombia researchers modelled factors that contribute to bird diversity and richness, reporting that the size of the forest path is key to both measures (Aubad et al., 2010). Richness, diversity and abundance decreased if the patch was easily accessible to humans (Aubad et al., 2010). Human disturbance was identified as important as patch size for species richness (Aubad et al., 2010).

The only study analysing effects of tourism, found evidence that tourists conversations have major disturbance in bird behaviour (Karp and Root, 2009).

In Colombia, researchers studied habitat characteristics that are related to snakes occupancy and determined that, in forests under the status of conservation, abundance doubled (Urbina-Cardona et al., 2008). In coconut plantations the abundance of snakes increased in the dry season. The highest
diversity was found in secondary forests near primary ones (Urbina-Cardona et al., 2008). In a beach in Venezuela, it was determined that *Dermochelys coriacea* behavioural nesting include looking for places with the lower disturbance and pollution of any type (Hernández et al., 2007).

In Ecuadorian Andes, researchers evaluated how resilient bird populations are to habitat degradation in a montane forest. They found that several factors contribute differently to the resilience capacity of species (O’Dea and Whittaker, 2007). Species richness was determined to be lower in agricultural landscapes, while, in some cases, species richness was the same as in primary forest (O’Dea and Whittaker, 2007). Species composition differed between secondary forest and forest edge. In the first case, there was a high abundance of forest specialized birds while in the second case it was a high abundance of forest and pasture birds (O’Dea and Whittaker, 2007).

In the Jatun Sacha Reserve in Ecuador, the abundance of amphibians increases with distance from pastures. No significant differences in amphibian abundance between primary and secondary logged forests was identified (Pearman, 1997). In Ecuador researchers determined that edge effect is strongly pronounced in frog populations. However, abundance remains stable in the forest and agricultural landscapes (Toral-Contreras et al., 2002).

Researchers have studied variations in population structure due to habitat fragmentation in *Geochelone carbonaria* and found significant differences in population structure in a non-fragmented habitat. More fragmented habitats are related with higher proportions of juvenile individuals in the population (Aponte et al., 2003).

In a study carried out in Colombia comparing agricultural and forest matrix, almost two thirds of analysed bird species showed significant differences in
abundance at both sites (Renjifo, 2001). Birds with more specific niche requirements showed less tolerance to habitat fragmentation in comparison to more generalist species (Renjifo, 2001). After long-term fragmentation, most vulnerable species became locally extinct and communities lost richness (Renjifo, 1999).

The age of the forest edge seems to be important to bird community composition (Restrepo et al., 1999). In younger forest edges the availability of fruits is higher with an increase in the abundance of frugivorous birds, while in old edges it seems not to be differences with other disturbed areas (Restrepo et al., 1999). During dry times, frugivores abundance seems to be higher in the forest interior than in the edges (Restrepo and Gómez, 1998). During the wet season insectivore abundance was higher in new edges than in old ones (Restrepo and Gómez, 1998). In Machalilla National Park in Ecuador, researchers determined that a high proportion of analysed birds are more likely to be found in the mature forest than in young forest (Becker and Ágreda, 2005). In second growth forest bird diversity was higher than it was in Garua forest (Becker and Ágreda, 2005).

In a study carried out with leptodactylid frogs in northern Ecuador, it was determined that while the abundance of one species of frogs seems to be affected by the size of the forest patch, other species did not present differences in abundance across forest patches of several sizes (Marsh and Pearman, 1997).

4.4 Discussion

This is the first time such a large systematic review has been conducted on the impact of habitat change on amphibians, reptiles and birds of North Western South America. The search led to the identification of 74 studies. Several
factors generate limitations to a SLR and omission of relevant citations cannot be avoided. Despite its large size, Scopus is a limited database and does not fully cover all publications ever produced. The wide scope of the study question makes it complex to capture all possible search term variations. Although Scopus includes several sources in Spanish, many publications presenting research done in Latin America are probably not included, and new databases such as Scielo or Redalyc could be included in the future.

There are clear geopolitical, geographic and thematic biases in the studies included in this review, with most research developed in montane slopes of Colombia. However, most sites appear to be repeatedly studied, which could be an effect of the ease of access, while large areas of north-western South America have been hardly monitored. Most information presented in this work refers to bird. Little information is available for amphibians and reptiles, and in particularly reptiles are little studied.

Studies presented in this review showed that human disturbance tend to generate reductions in abundance and richness of reptiles and amphibians. Results of the same disturbance seems to differ according to taxa, with birds appearing to have a better adaptation capacity to human disturbance than other taxa. Research shows that different guilds of birds have a broad variety of responses to human impact. Frugivorous birds seem to be favoured in silvopastoral landscapes, while granivorous birds seem advantaged in pasture systems. The effect of land cover is usually negative for insectivorous birds, but the effect of land use on this group of birds is unclear.
References


Aguilar, J. M. et al. (2016) Rapid colonization of Ecuador by the Tropical Mockingbird (Mimus gilvus. Ornitología Neotropical. 27 (0), 155–162.


Appendices

Appendix 1 Search terms

Search terms of the Systematic Literature Review of impacts of habitat change on amphibians, reptiles and birds of the Neotropical region. Final search string: (#1 OR #2 OR #3 OR #4 OR #5) AND #6 AND #7.

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<td>(+ population)</td>
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<td>Amphibians</td>
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Birds
(+ population)

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## Appendix 2 List of references used for the evidence synthesis.

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Chapter 5  Impacts of human-driven habitat change on amphibians and reptiles of north-western South America
5.1 Introduction

Biodiversity comprises all variability among living organisms, including the diversity within and between species as well as the ecological complexes to which they belong and with which they interact—with each other and their physical environment (Groves et al., 2002; Mace et al., 2012; Purvis and Hector, 2000; Secretariat CBD, 2010). Biodiversity provides important use and non-use values to humanity many of which we have derived into ecosystem services (Ehrlich and Ehrlich, 1992; Mace et al., 2012). Human societies have always depended on ecosystem services, from provision of food to climate control or formation of fertile soils, among others, but their significance has often been poorly appreciated (Boyd and Banzhaf, 2007; Costanza, 2008; Fisher and Kerry Turner, 2008; Fisher et al., 2009; Mace et al., 2012; Secretariat CBD, 2010; Wallace, 2007).

Geological and ecological processes have driven major biodiversity changes. These processes are extrinsic to life evolution and remain important drivers of biodiversity change (see Chapters 1 and 2). Biodiversity changes can also be explained by the influence of past and present human impacts. Humans have modified the configuration and extent of ecosystems since prehistoric age (Williams, 2003; FAO, 2016b). However, over the past two centuries, humans have become a global force able to change natural ecosystems at rates previously unseen (Mace et al., 2005; Sala et al., 2000; Secretariat CBD, 2014). Human-driven processes have biodiversity under considerable stress and it has been suggested that rates of biodiversity extinction are close to a mass extinction event (Barnosky et al., 2011; Ceballos et al., 2015, 2017; McCallum, 2015). The most important direct processes currently driving significant biodiversity changes are human-driven and include: habitat change, invasive alien species and introduced pathogens, overexploitation, climate change, and their synergic interactions (Alford and Richards, 1999; Andrén, 1994; Brook, 2008; Brook et al., 2008; Daszak et al., 2001, 2000; Debinski and Holt, 2000; Everett, 2000; Fahrig, 2003; Foley et al., 2005, 2007; Gardner et al., 2007;
among all threats to biodiversity, habitat change—also called landscape change/modification, has been identified as the most widespread, with extensive impacts on terrestrial, freshwater and marine ecosystems (Mace et al. 2005; Secretariat CBD 2006, 2010; UN, 2014; IUCN, 2014a, Sala et al. 2000).

Habitat change includes a set of complex and cross-temporal multi-factors (Chazdon, 2014; Fahrig, 2003; Fischer and Lindenmayer, 2007; Lindenmayer and Fischer, 2013). Among the most common causes of human-driven habitat change are agricultural expansion, infrastructure development, and urbanisation (Lindenmayer and Fischer, 2013; FAO, 2016b). Spatial succession patterns of habitat change usually include processes of perforation, dissection, fragmentation, shrinkage, and attrition of native vegetation. Such processes produce a land matrix dominated by a variety of anthropogenic land uses (Ewers and Didham, 2006; Fahrig, 2003).

Habitat change is a serious problem threatening global biodiversity and causing decline and extinction events that gravely jeopardize the long-term survival of all taxonomic groups and thousands of species, including humans (Fischer and Lindenmayer, 2007; Foley et al., 2005; Sala et al., 2000; Secretariat CBD, 2014, 2010). Disturbance to biodiversity due to habitat change may decrease the resilience of ecosystems and threaten the services they provide to humans (Ehrlich and Ehrlich, 1992; Mace et al., 2012; Secretariat CBD, 2014, 2010). Habitat change is the second largest source of human-mediated CO2 emissions (IPCC, 2014).

Habitat loss and fragmentation due to deforestation, two of the most studied types of habitat change, have decreased Earth’s original (i.e., pre-human impact) forested areas by ca. 15–25% (Klein Goldewijk et al., 2011; Williams, 2003, 2000; FAO, 2016b). Deforestation, for the development of agricultural
lands, dates back thousands of years, and a complex cycle of decline and recovery of vegetation cover has occurred due to changes in human pressures (Chazdon, 2014; Levis et al., 2017; Lindenmayer and Fischer, 2013; Redman, 1999; FAO, 2016b). However, a deforestation peak occurred during the 20th century, when deforestation diverged from temperate regions to tropical regions (Williams, 2003). In the 21st century, while net forested areas have increased in temperate areas in recent years, net annual loss of forests in tropical areas was ca. 70000 km² from 2000 to 2010 (FAO, 2016b). Most of habitat loss in the first decade of the 21st century occurred in South America, sub-Saharan Africa, and southern Asia. The main drivers were large-scale commercial cropland (40%), local subsistence agriculture (33%), and urban expansion, infrastructure and mining (27%) (Keenan et al., 2015; Sloan and Sayer, 2015; FAO, 2016b).

In South America, forested areas declined to around 50% of the land area by the end of the 20th century, and there was a further decrease of 5.48% between 2000 and 2015 (FAO, 2016a, 2016b; Keenan et al., 2015). Habitat change, mainly forest loss, in South America has been extensively studied (Achard et al., 2014; Clark et al., 2012; Eva et al., 2012; Geist and Lambin, 2002; Graesser et al., 2015; Hansen et al., 2013; Hosonuma et al., 2012; Houghton, 2012). Habitat change in South America is strongly correlated with expansion of the agricultural frontier. However, different types of agricultural and non-agricultural drivers have heterogeneous patterns of magnitude and spatial-temporal distribution across South America (De Sy et al., 2015).

Species biodiversity is greatest in the tropics and all countries in north-western South America (NWSA, see Chapter 2 for definition) have been identified as megadiverse, harbouring the majority of Earth's species (Mittermeier et al., 1997). NWSA shows regional variation, and while most South American countries showed net gain in agricultural areas and net loss in forested areas, Ecuador and Colombia, the two main countries in NWSA, had net loss in forested areas and in agricultural areas (FAO, 2016a). While pasture expansion of cattle ranching is the main driver of habitat change
across NWSA, smallholder cropland and mixed agriculture expansion are also dominant in the region (De Sy et al., 2015). In NWSA, infrastructure development and commercial crops contribute little as proximate drivers of habitat changes at national levels, although may be representative at local levels (De Sy et al., 2015; IDEAM and MADS, 2014; MAE, 2014).

Habitat change is slowing in NWSA, due to national regulations and in-situ conservation strategies (mainly expanding protected-areas systems), but NWSA continues to experience significant habitat losses (Keenan et al., 2015). Across tropical areas, natural regeneration and silvopasture systems are becoming increasingly prevalent (Chazdon et al., 2009; Meyfroidt and Lambin, 2011; Schnell et al., 2015). In South America, spontaneous forest regrowth on abandoned agricultural lands and silvopasture systems increased over the 2000s according to satellite estimates (Aide et al., 2013; Asner et al., 2009; Sloan and Sayer, 2015). Despite several studies showing the significant impacts of habitat changes on herpetofauna—i.e., amphibians and reptiles (Cushman, 2006; Gardner et al., 2007), regional and national studies in Ecuador suggest that habitat change is not a major factor related with population declines in amphibians (Alan Pounds et al., 2006; Menéndez-Guerrero and Graham, 2013; Ron et al., 2003; Young et al., 2001).

The aim of this research is to improve knowledge on the impacts caused by human-driven habitat changes on the biological diversity and to evaluate the efficiency of in-situ conservation initiatives to mitigate negative impacts. I generated evidence to understand the impacts caused by habitat changes on species richness and endemism of north-western South America by using a multi-taxonomic approach, including data from amphibians and reptiles. I analysed a complex array of species with heterogeneous ecological characteristics and conservation status. The analysis includes updated data on amphibian diversity and provides for the first time a comprehensive evaluation of reptiles of the region. With these outputs, I evaluated the potential of natural protected areas, as in-situ conservation strategies in the
region, to mitigate impacts of habitat change at all levels (geographic, ecological and taxonomic).

5.2 Methodology

5.2.1 Study area

This study was centred in mainland north-western South America (NWSA), which includes the Northern Andes and all adjacent lowland environments. A review, definition, and description of NWSA is provided in Chapter 2. Since in-situ conservation decisions are directly enforced by national governments, which take effect at national borders, the analyses herein presented will be restricted to the national boundaries of Colombia and Ecuador. Due to the current political situation and lack of access to scientific collections, Venezuela was excluded from this study.

5.2.2 Study taxa and species selection

This study is based on distributional data of two clades of terrestrial vertebrates: amphibians and reptiles, from a compilation completed in 2015 and partly adjusted to account for subsequent taxonomic revisions. I included only species of the clades Anura and Caudata, thereby excluding the little-known caecilians. I use the general term “amphibians” to refer to these group. I use the term "reptiles" in its classical meaning, i.e., reptiles are all non-avian reptiles, including squamates, chelonians and crocodylians. I restricted this study to species of the clade Squamata (i.e., lizards and snakes).

These groups were selected based on the following criteria: (i) they have been studied extensively and their systematics are fairly well understood; (ii) their solved taxonomies allow correct identification of voucher specimens deposited in museum collections; (iii) expeditions recently conducted have resulted in significant knowledge increase regarding the distribution of most species; (iv) they show a significant variety of morphological, behavioural, physiological, and ecological features, thus representing an interesting
heterogeneous group to assess biogeographic patterns at a wide zoogeographic scale; and (v) I have significant taxonomic expertise, field experience, and geographic knowledge of all three clades in NWSA.

I compile a complete species lists of amphibians and reptiles of NWSA, using the following databases: The Reptile Database (Uetz and Hošek, 2015), and Amphibian Species of the World: an Online Reference (Frost, 2015). Where taxonomic hypotheses proposed opposed views on the nomenclature or species definitions, I adopted the most recent evidence-based taxonomic contribution. Subsequently, I selected species that matched the following criteria: (i) at least one valid vouchered record within the geographic boundaries of the study region, with valid vouchers interpreted as verifiable photographs, song recordings or museum specimens; (ii) with objective and well-defined taxonomic identity, enough as to assign valid vouchered records with confidence; (iii) with resident breeding established populations in NWSA, thus excluding all migratory, vagrant, or species without established populations in NWSA; (iv) with locality-points that validate a specific land habitat occurrence, thus excluding all species which are exclusively aquatic, or where most records correspond to individuals dispersing over air or water, but without certainty about its presence in a specific locality-point, thus excluding all species such as turtles or swifts which are predominantly aquatic and aerial respectively. I only included well-defined, scientifically described species. Given that the number of undescribed species keeps increasing and their status changes alongside of taxonomic revisions, my dataset represents a snapshot of taxonomic knowledge from 2015, with some updates. While changing taxonomy in some clades, incomplete geographic information, and exclusion of some species at the time of compilation of my dataset may lead to biased representations of species richness and endemism in some groups, they nevertheless do not invalidate general patterns reported herein.
5.2.3 Data collection

I collected species occurrence datasets for each study group: anuran amphibia and squamate reptiles from mainland regions of the Northern Andes. Occurrence data were obtained from different structured and semi-structured data sources. I used the following sources of species occurrence data: (i) scientific literature, (ii) 21 natural history museums, (iii) open-data biodiversity databases, and (iv) private expert databases, including my own data collected during fieldwork. Data extraction from all these sources was conducted between January 2013 and December 2015. A detailed description of methodologies used for data collection is presented in Chapter 3.

A significant amount of information about the amphibians and reptiles of north-western South America remains unpublished and in private databases of expert herpetologists and ornithologists. In order to collect information kept in private expert databases, I contributed to the organisation of workshops which were part of the global assessments for The IUCN Red List of Threatened Species and were organised in collaboration with The International Union for Conservation of Nature IUCN, NatureServe (with the support from the National Science Foundation’s Dimensions of Biodiversity program, award 1136586), the IUCN-SSC Amphibian Specialist Group, Universidad San Francisco de Quito USFQ, and the Asociación Colombiana de Herpetología. I was appointed as coordinator for Ecuador of the Amphibian Red List Authority and of the Snake and Lizard Reptile Red List Authority. Three workshops were organised to assess squamate reptiles: Medellin, 21–25 October 2013; Quito, 24–27 February 2014; and Quito, 22–26 November 2014; and one workshop for amphibians: San Isidro, 16–19 July 2016. While these workshops updated information for amphibians and birds from previous assessments, they also compiled new data and evaluated the information available for all species. The reptile workshops were the first comprehensive assessments of NWSA reptile richness and conservation status.
5.2.4 Data structure

All compiled locality-point data were stored with the standardise basic data structure of a record in a Microsoft Excel spreadsheet, to minimise data heterogeneity. The record for each study taxa contains the following fields: (i) Scientific name, with the format “Genus species”; (ii) locality; (iii) source code, when available, e.g. museum codes or database code; (iv) latitude, in decimal degrees; (v) longitude, in decimal degrees; (vi) altitude, in metres; (vi) source reference; and, (viii) observations. Fields “locality”, “latitude”, “longitude” and “altitude” were initially filled with the verbatim information available from the original source of the record. They were subsequently modified, when needed, according to the data curation protocol to lower the amount of data variation, which could affect its interpretation.

5.2.5 Data curation and data mining

Different sources used for this study represented a significant and heterogeneous volume of data to be managed. Since most species had few occurrence records (<25 locality-points), every record was critical data. I established a protocol for data curation and data mining divided into several stages, which provided a methodological and technological data management support to address data quality issues and to maximise data use and future re-use (Freitas and Curry, 2016): (i) occurrence records validation, (ii) duplicate selection, (iii) taxonomic validation, (iv) georeferencing process, (v) preliminary map building, (vi) critical map assessment, (vii) final map building and calculation of extent of suitable habitat before human-driven habitat change (ESH$_0$), (viii) diversity and endemicity analyses, (ix) biogeographic analyses, (x) calculation of extent of suitable habitat after human-driven habitat change (ESH$_H$), (xi) classification of species based on habitat typology, (xii) calculation of ESH$_0$ and ESH$_H$ in state-owned and private protected areas. A detailed description of stages (i) to (ix) used for data curation and mining is presented in Chapter 3. These first stages were applied to calculate the extent of suitable habitat without human-driven habitat...
change (ESH₀), which are herein considered as the maximum potential areas of occupancy of each species (Beresford et al., 2011). The major difference between ESH₀ and simple “ESH” commonly used in other studies (e.g., Beresford et al., 2011; Brummitt et al., 2016; Di Marco et al., 2013) is that habitat changes produced by humans are left out of the calculation of ESH₀. Human-driven habitat changes will be included in following calculations. Stages (x) to (xii) of data mining were developed as described below.

5.2.5.1 Calculation of extent of suitable habitat after human-driven habitat change (ESH_H)

I built a dataset of human-driven habitat changes for Colombia and Ecuador — generated for this study, based on the following sources: classification system of the vegetation of Ecuador (Sierra M., 1999), classification system of the ecosystems of mainland Ecuador (MAE et al., 2012, 2013), deforestation baseline of mainland Ecuador (MAE, 2012), land cover and land use map of Ecuador (MAGAP, 2012), transformed areas of the Amazonia of Colombia (SINCHI, 2012), land cover Amazonia 2014 (SINCHI, 2014a), map of forest/non-forest of Colombia (IDEAM, 2013), 2002-2014 degraded forests of Colombia (SINCHI, 2014b), ecosystems of Colombia (IAvH, 2012). The dataset was generated including all pixels assigned in the sources to any type of human-driven habitat change, including: land conversion into agricultural lands, urban centres and urban sprawl, infrastructure development, logging, and degraded and abandoned lands. Special care was taken to avoid inclusion of natural open areas, such as wild grasslands (including paramo highlands and savannas) and dry scrublands. This map was created on the assumption that identical native vegetation cover classes were used across the sources. All species were clipped using this map with the Clip function in the Geoprocessing toolset available for ArcGis 10.4® 10.4 by ESRI. The resultant species ranges were classified as the extent of suitable habitat after human-driven habitat change (ESH_H).
5.2.5.2 Classification of species based on habitat typology

Species were classified as (i) forest species and (ii) non-forest species, based on information available for the species in the literature, textual information on habitat preferences from the IUCN Red List (IUCN, 2016) and personal field experience. Non-forest species included all habitat generalists that use forested and open habitats, including human-modified scrublands and grasslands. In order to evaluate the level of adaptation of non-forest species, I used the conceptual model of habitat modification states of McIntyre and Hobbs (1999) (Figure 15) (A) Intact habitat, with little or no alteration (>90% remaining native cover), high habitat connectivity, low modification, and a mosaic of ecosystems with gradients. (B) Variegated habitat, with moderate alteration (60–90% remaining native cover), high connectivity in general, but low for species sensitive to habitat modification, low to high modification, and a mosaic of ecosystems with gradient and abrupt boundaries. (C) Fragmented habitat, with high alteration (10–60% remaining native cover), generally low connectivity, low to high modification, and ecosystem gradients with fragments. (D) Relictual habitat, with extreme alteration (<10% remaining native cover), no connectivity, highly modified, and generally uniform ecosystems. As habitat change increases, ecosystems are modified by native vegetation cover reduction and land use intensity and increased disturbances to surrounding native areas are produced by processes originating in modified areas (Fischer and Lindenmayer, 2007; Lindenmayer and Fischer, 2013; McIntyre and Hobbs, 1999). In reference to Figure 15, all species that inhabit states A and B were classified as forest species, while species that inhabit states C and D were classified as non-forest species.
Conceptual model of habitat modification states (see text, modified from McIntyre and Hobbs, 1999). (A) Intact habitat, (B) Variegated habitat, (C) Fragmented habitat, (D) Relictual habitat. Images accessed through Google Earth: Google (2018), CNES/Airbus (2018), Digital Globe (2018), U.S. Geological Survey. (A) 0°29'56.40" S, 76°06'54.85" W, 230 m elevation, Amazonian lowlands, Ecuador; (B) 0°54'09.08" S, 76°49'39.05" W, 290 m elevation, Amazonian lowlands, Ecuador; (C) 0°18'09.81" S, 76°47'58.45" W, 280 m elevation), Amazonian lowlands, Ecuador; (D) 0°58'38.80" S, 79°42'40.15" W, 70 m elevation, Pacific lowlands, Ecuador.

Figure 15 Conceptual model of habitat modification states
5.2.6 Importance of state-owned and private protected areas

I analysed in-situ conservation initiatives in the form of protected areas. I studied which species richness and endemism is protected by the current system of protected areas. Gap analyses were conducted for amphibians and reptiles versus geographic areas and extinction risk category using both simple and compositionalist stacking. Simple stacking involves simple addition of all obtained maps across the study region and to analyse the diversity of all areas within the region at once. Compositionalist stacking involves dividing the study region into smaller biogeographic areas, each one with a specific pool of species that differ from the pools of other areas, to standardise the diversity of each areas as values between 0 and 1, and then add this standardised information into a final regional map. ESH$_0$ and ESH$_H$ of all species were clipped using the official maps of state-owned and private protected areas of Colombia (SPNN, n.d.) and Ecuador (MAE, 2015b, 2015a) with the Clip function in the Geoprocessing toolset available for ArcGis 10.4® 10.4 by ESRI.

5.2.7 Data Analysis

I used one-way ANOVA with Tukey-Kramer post-hoc test. In cases where heteroscedasticity was high, I used Welch’s ANOVA with Games-Howell post-hoc test. Bartlett’s test was used to test homoscedasticity. Before analysis, data was 10-log transformed to reduce skewness and improve homoscedasticity. Partial regression plots were used to represent the relationship between the dependent and each explanatory variable, while keeping the other variables constant (Maindonald and Braun, 2006).

5.2.8 Identification of species with underestimated extinction risk

I used the ESH$_0$ and ESH$_H$ to identify species for which the extinction risk is likely underestimated in the IUCN Red List of Threatened Species (IUCN, 2016) following the method proposed by (Ficetola et al., 2015). Thus, I assumed that forest species with ESH$_H$ less than 20 km$^2$ and potential future
threats are potentially Vulnerable VU according to criterion D2. Also, species might qualify for the following categories under criterion B2: $\text{ESH}_T < 10 \text{ km}^2$ for potential status of Critically Endangered CR, $\text{ESH}_T < 500 \text{ km}^2$ for potential status of Endangered EN, and $\text{ESH}_T < 2000 \text{ km}^2$ for potential status of Vulnerable VU, as long as there are reports of ongoing decline or severely fragmented range by human-driven habitat change as showed by the $\text{ESH}_T/\text{ESH}_0$ ratio.

5.3 Results

5.3.1 Extent of Suitable Habitat without Human-driven Habitat Change ($\text{ESH}_0$)

Average $\text{ESH}_0$ was smaller in amphibians ($52737.09 \pm 128643.30 \text{ km}^2$, n = 914 spp.) than in reptiles ($144516.91 \pm 248956.94 \text{ km}^2$, n = 564 spp.); showing significant differences between both clades ($t = 6.23$, 1476 d.f., $p < 0.0001$). Differences of $\text{ESH}_0$ of amphibians and reptiles among biogeographic regions were also significant (for amphibians: $F_{2, 1790} = 23.395$, $p < 0.0001$; for reptiles: $F_{2, 1008} = 68.283$, $p < 0.0001$; Tukey-Kramer test, $p < 0.05$). The exception was for amphibians, between Cis-Andean and High Andean regions that share small average $\text{ESH}_0$ (Tukey-Kramer test, $p > 0.05$).

Non-forest amphibians had larger $\text{ESH}_0$ ($152379.78 \pm 207068.23 \text{ km}^2$, n = 205 spp.) than forest amphibians ($23926.44 \pm 72665.97 \text{ km}^2$, n = 709 spp.). Differences between these ecological guilds were strongly significant ($F_{1, 395.71} = 302.47$, $p < 0.0001$). Although non-forest reptiles had larger $\text{ESH}_0$ ($198462.04 \pm 260920.62 \text{ km}^2$, n = 105 spp.) that forest reptiles ($132176.53 \pm 244765.10 \text{ km}^2$, n = 459 spp.), differences were hardly significant ($F_{1, 148.72} = 5.641$, $p = 0.0188$).

Average $\text{ESH}_0$ strongly varied among amphibians assigned to different IUCN categories ($F_{5, 268.71} = 133.63$, $p < 0.0001$). Post hoc comparison analysis indicated that all categories differed on the amount of $\text{ESH}_0$. Species classified in threatened categories had significantly smaller $\text{ESH}_0$ (CR: $1974.74 \pm 4428.92 \text{ km}^2$, EN: $2803.42 \pm 5656.783 \text{ km}^2$, VU: $8005.38 \pm 16041.23 \text{ km}^2$) than species in
non-threatened categories (NT: 14784.18 ± 17987.23 km², LC: 122535.62 ± 180456.69 km²) (Games-Howell test, p < 0.05). The exception was for Data Deficient amphibians (4645.43 ± 18220.36 km²), which showed no significant differences with CR and EN species (Games-Howell test, p > 0.05).

Differences among IUCN categories were also strong in reptiles ($F_{5,66.201} = 135.679$, p < 0.0001). Post hoc comparison analysis showed that species classified in threatened categories had significantly smaller $E_{S0}$ (CR: 315.55 ± 433.44 km², EN: 2200.56 ± 4018.17 km², VU: 10768.71 ± 16289.24 km²) than species on non-threatened categories (NT: 16930.27 ± 20806.00 km², LC: 234604.58 ± 285536.00 km²) (Games-Howell test, P < 0.05). Reptiles classified as Data Deficient (2287.44 ± 10094.07 km²) showed no significant differences with CR species (Games-Howell test, p > 0.05).

5.3.2 Extent of Suitable Habitat after Human-driven Habitat Change ($E_{SH}$)

$E_{S0}$ and $E_{SH}$ of amphibians were strongly correlated ($r^2 = 0.987, 906$ d.f., p < 0.0001), but $E_{SH}$ were significantly smaller than $E_{S0}$ ($t = 3.24, 1814$ d.f., p = 0.0012). Similar trends were found in reptiles ($r^2 = 0.981, 559$ d.f., p < 0.0001; $t = 2.85, 1120$ d.f., $P = 0.004$). Average $E_{SH}$ was significantly smaller in amphibians (44539.90 ± 115536.06 km², n = 914 spp.) than in reptiles (117787.87 ± 212706.00 km², n = 564 spp.) ($t = 5.07, 1467$ d.f., p < 0.0001).

Forest amphibians had smaller $E_{SH}$ (122724.31 ± 187413.80 km², n = 170 spp.) than non-forest amphibians (15278.87 ± 60096.09 km², n = 589 spp.), and these differences were strongly significant ($F_{1,757} = 186.24$, p < 0.0001). Similar patterns were observed in reptiles, with significant differences between $E_{SH}$ of forest species (151353.94 ± 217956.53 km², n = 105 spp.) and non-forest species (110833.76 ± 211482.38 km², n = 456 spp.) ($F_{1,224.68} = 43.75$, p < 0.0001).

After considering variations in range size, human-driven habitat change impact was higher in amphibians and reptiles with smaller $E_{S0}$ (Figure 16 and Figure 21). Threatened amphibians and reptiles (i.e., those assigned to IUCN threatened categories CR, EN and VU) had stronger impacts of human-
drive habitat change than non-threatened species ($F_{1,699.05} = 32.526$, $p < 0.0001$). Impacts of habitat change show opposed trends based on IUCN categories, with higher impact on threatened amphibians and reptiles with larger ESH$_H$, but lower in widely distributed non-threatened species (Figure 17 and Figure 22). Amphibians and reptiles assigned to different IUCN categories had strongly different ESH$_H$ ($F_{5,267.43} = 132.43$, $P < 0.0001$ for amphibians; $F_{5,38.132} = 68.232$, $P < 0.0001$ for reptiles). ESH$_H$ of threatened amphibians were significantly smaller (CR: $1080.20 \pm 2340.39$ km$^2$, EN: $1760.21 \pm 3506.15$ km$^2$, VU: $4672.43 \pm 9502.20$ km$^2$) than non-threatened species (NT: $9015.60 \pm 10435.05$ km$^2$, LC: $105623.50 \pm 163910.3$ km$^2$) (Games-Howell test, $P < 0.05$). ESH$_H$ of amphibians classified as Data Deficient ($3834.83 \pm 17370.29$ km$^2$) were similar to species in CR and EN categories (Games-Howell test, $P > 0.05$) (Figure 18). In reptiles, threatened species had smaller ESH$_H$ (EN: $1326.95 \pm 1710.81$ km$^2$, VU: $7610.43 \pm 13144.43$ km$^2$) than non-threatened species (NT: $9276.63 \pm 12593.41$ km$^2$, LC: $106408.69 \pm 181873.60$ km$^2$), although there were no significant differences between the following categories: NT-EN, NT-VU, EN-VU. ESH of reptiles classified as Critically Endangered (CR: $88.18 \pm 116.90$ km$^2$) were significantly smaller than those in all other categories (Games-Howell test, $P < 0.05$). ESH$_H$ of amphibians classified as Data Deficient were not significantly different from those classified as Critically Endangered (Games-Howell test, $P > 0.05$).

Differences of ESH of amphibians in Cis-Andean regions were significant when compared with those of High-Andean and Trans-Andean regions ($F_{2,670.93} = 54.223$, $P < 0.0001$), but Trans-Andean and High Andean regions were not significantly different (Tukey-Kramer test, $P > 0.05$). Differences of ESH of reptiles across all regions were significant ($F_{2,527.53} = 73.084$, $P < 0.0001$; Games-Howell test $< 0.05$). In average, Imeri and Sabana were the biogeographic provinces with the least amount of human-driven habitat change, while Western Ecuador, Ecuadorian, Guajira and Magdalena report the greatest impacts (Figure 19 and Figure 20).
Figure 16  Regression plot showing the relationship between proportion of habitat change and extent of suitable habitat (ESH) of amphibians from north-western South America.
Regression plot showing the relationship between proportion of human-driven habitat change and extent of suitable habitat before human-drive habitat change (ESH₀) in amphibians from north-western South America, according to their IUCN threatened categories. Black diamonds and dashed lines correspond to threatened species categorised in the following categories: Critically Endangered CR, Endangered EN, and Vulnerable VU. Circles and dotted line correspond to non-threatened species categorised in the following categories: Near Threatened NT and Least Concern LC.

Figure 17 Regression plot showing the relationship between proportion of human-driven habitat change and extent of suitable habitat before human-drive habitat change (ESH₀) in amphibians from north-western South America
Regression plots showing the relationship between proportion of habitat change and range size of forest-dependent amphibians for each IUCN category (CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient). Black bars show the average proportion of habitat change for each category. Horizontal axis corresponds to 10log-transformed ESH.

**Figure 18** Regression plots showing the relationship between proportion of habitat change and range size of forest-dependent
Figure 19  Proportion of habitat change impacting amphibians among biogeographic provinces of north-western South America.
Figure 20  Proportion of habitat change impacting squamate reptiles among biogeographic provinces of north-western South America.
Figure 21  Regression plot showing the relationship between proportion of habitat change and extent of suitable habitat (ESH) of squamate reptiles from north-western South America
Figure 22  Regression plot showing the relationship between proportion of human-driven habitat change and extent of suitable habitat before human-drive habitat change (ESH0) in squamate reptiles from north-western South America.
Regression plots showing the relationship between proportion of habitat change and range size of forest-dependent squamate reptiles for each IUCN category (CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient). Black bars show the average proportion of habitat change for each category. Horizontal axis corresponds to 10log-transformed ESH.

**Figure 23** Regression plots showing the relationship between proportion of habitat change and range size of forest-dependent squamate reptiles
Figure 24  Histograms showing the cumulative number of species of amphibians based on the percentages of ESH₀ included in state-owned protected areas (top) and private protected areas (bottom)
5.3.3 Detection of potential threatened species currently classified as Data Deficient

I identified 16 species of forest amphibians and 15 species of forest reptiles currently classified as Data Deficient DD for which current extinction risk may be underestimated. In addition, two amphibian species currently classified as DD might qualify for Near Threatened.

One species of amphibian and five species of reptiles potentially have less than $20 \text{ km}^2$ of $\text{ESH}_H$ and high impacts by human-driven habitat change, thus might be considered Vulnerable VU according to Criterion D2. Two DD amphibian species might be classified as Critically Endangered; 12 DD amphibians and six reptiles as Endangered EN, and one amphibians and five reptiles as Vulnerable VU, due to their small $\text{ESH}_H$ and ongoing and high impacts due to human-driven habitat change. Also, 10 amphibian species and 21 reptile species that are currently known only from their type localities might also be threatened, since high impact of human-driven habitat change was detected in their known distribution areas and surroundings.
Table 3. Anuran amphibian species from north-western South America currently classified under the Data Deficient IUCN category and identified as potentially threatened

Anuran amphibian species from north-western South America currently classified under the Data Deficient IUCN category and identified as potentially threatened. Current and candidate columns refer to IUCN categories. Asterisks indicate species that despite being known only from their type localities, are potentially threatened due to high impacts of human-driven habitat change.

<table>
<thead>
<tr>
<th>Species</th>
<th>Current</th>
<th>Candidate</th>
<th>ESH₀</th>
<th>ESH₁</th>
<th>% Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ameerega andina</td>
<td>DD</td>
<td>EN B2</td>
<td>50.27</td>
<td>20.16</td>
<td>0.60</td>
</tr>
<tr>
<td>Atelopus guitarraensis</td>
<td>DD</td>
<td>EN B2</td>
<td>65.82</td>
<td>21.15</td>
<td>0.68</td>
</tr>
<tr>
<td>Atelopus sanjosei</td>
<td>DD</td>
<td>EN B2</td>
<td>350.82</td>
<td>162.57</td>
<td>0.54</td>
</tr>
<tr>
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<td>DD</td>
<td>CR B2</td>
<td>54.21</td>
<td>11.00</td>
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</tr>
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<td>65.94</td>
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<tr>
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<td>16.65</td>
<td>0.80</td>
</tr>
<tr>
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<td>ESH₁</td>
<td>% Change</td>
</tr>
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<td>EN B2</td>
<td>756.87</td>
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</tr>
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Table 4.  **Squamate reptile species from north-western South America currently classified under the Data Deficient IUCN category and identified as potentially threatened**

Squamate reptile species from north-western South America currently classified under the Data Deficient IUCN category and identified as potentially threatened. Current and candidate columns refer to IUCN categories. Asterisks indicate species that despite being known only from their type localities, are potentially threatened due to high impacts of human-driven habitat change.

<table>
<thead>
<tr>
<th>Species</th>
<th>Current</th>
<th>Candidate</th>
<th>ESH₀</th>
<th>ESHᵢ</th>
<th>% Change</th>
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<td>ESHᵣ</td>
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</tbody>
</table>
5.3.4 **Protected Areas**

The largest protected areas have been established in the Cis-Andean region of north-western South America, especially on the Amazonian lowlands; e.g., Reserva Nacional Natural Puinawai and Parque Nacional Natural Sierra de Chiribiquete in Colombia, and Parque Nacional Yasuní and Reserva de Producción Faunística Cuyabeno in Ecuador (Appendix 3 and 4). On the High Andes region, a combination of mid-size and small protected areas protects a larger percentage of Cordillera Oriental of Colombian and Cordillera Real of Ecuador, than of Cordillera Central of Colombia and Cordillera Occidental. Several protected areas across the High Andes of southern Cordillera Oriental of Colombia and Cordillera Real of Ecuador form a fairly continuous corridor; i.e., Parque Nacional Natural Serranía de los Churumbelos in Colombia, and Parque Nacional Cayambe-Coca, Parque Nacional Sumaco Napo Galeras, Reserva Ecológica Antisana, Parque Nacional Llanganates, and Parque Nacional Sangay in Ecuador. On the Cordillera Central of Colombia and Cordillera Occidental of Colombia and Ecuador, only the following protected areas preserve medium-sized tracks of continuous native ecosystems: Parque Nacional Natural Serranía de San Lucas and Parque Nacional Natural Nudo de Paramillo of Colombia, and Reserva Ecológica Cotacachi Cayapas and Reserva Ecológica Los Illinizas. The Trans-Andean region of north-western South America shows the lowest concentration of protected areas, which are usually small in comparison with those of other regions. The largest protected areas are on the Pacific lowlands of Colombia and Ecuador, and include Parque Nacional Natural Sanquianga in Colombia, and Reserva Ecológica Mache Chindul and Parque Nacional Machalilla in Ecuador. The Caribbean lowlands of Colombia are largely void of protected areas, except for the Parque Nacional Natural Sierra Nevada de Santa Marta that covers the homologous mountain range.

State-owned protected areas cover larger areas than private protected areas (except for the Achuar and Huaorani communal protected forests in the
Amazonian lowlands of Ecuador). State-owned protected areas included—partially or totally—the ESH\(_0\) of 786 spp. of amphibians (86% of species included in this study) and 476 spp. (84%) of squamate reptiles. Private protected areas covered 723 spp. of amphibians (79%) and 466 spp. (83%) of reptiles. State-owned protected areas included larger ESH\(_0\) of amphibians (10514.04 ± 25994.00 km\(^2\)) than private protected areas (4748.02 ± 8293.13 km\(^2\)), but differences were not significant. However, a significantly higher proportion of ESH\(_0\) was included by state-owned protected areas (22.34%) than private protected areas (17.43%) (F\(_{1, 1506.97}\) = 18.266, P < 0.0001). State-owned protected areas preserved larger proportions (82.35%) of ESH\(_0\) (i.e., less extensive changes between ESH\(_{14}\) and ESH\(_0\)) than private protected areas (78.22%) (F\(_{1, 1484}\) = 13.698, P < 0.001). Differences were larger when only forest amphibians were accounted (85.00% of ESH\(_0\) in state-owned protected areas versus 78.35% in private protected areas; F\(_{1, 1058.14}\) = 28.90, P < 0.0001).

Human-driven habitat change has been more intense outside of protected areas in north-western South America. Since the Amazonian lowlands are characterised by having higher species richness of amphibians and reptiles, large protected areas in the region have helped preserve diversity of amphibians and reptiles from human-induced habitat change (e.g., Parque Nacional Yasuni). However, the large absence or spatial coverage of protected areas in the Trans-Andean and High-Andean regions have left areas of high species richness without protection (e.g., the River Magdalena Valley and the Pacific lowlands of western Colombia and north-western Ecuador). In terms of endemic species richness of amphibians and reptiles, most areas with high concentration of endemic species are left outside of protected areas, and human-driven habitat change has already impacted most of the ecosystems in the Western Ecuador and Ecuadorian biogeographic provinces. Five protected areas are important for the preservation of endemic species: Parque Nacional Farallones de Cali in the Cordillera Occidental of Colombia, Reserva Ecológica Cotacachi Cayapas, Reserva Ecológica Mache Mindul and Parque Nacional
Machalilla in the Pacific lowlands of Ecuador, and Parque Nacional Sumaco Napo Galeras in the Amazonian foothills of Ecuador.

For reptiles, state-owned protected areas encompassed significantly larger ESH of species ($27236.24 \pm 45098.15 \text{ km}^2$) than private protected areas ($8021.35 \pm 11170.41 \text{ km}^2$) ($F_{1, 534.26} = 81.315, P < 0.0001$). While state-owned protected areas included a slightly larger proportion of ESH of species (14.34%) than private protected areas (12.51), although differences were not significant. However, state-owned protected areas preserved larger proportions (83.00%) of ESH than private protected areas (74.00%) ($F_{1, 926.72} = 41.467, P < 0.0001$), but when only forest reptiles were accounted for, differences were not larger (82.56% versus 73.47%), but remained significant ($F_{1, 839.59} = 37.366, P < 0.0001$).

ESH of 125 species of amphibians and 50 species of reptiles coincide exclusively with state-owned protected areas, while 59 species of amphibians and 39 species are only included in private protected areas (Appendix 1, Appendix 2). In both cases, they contain a high proportion of threatened species. Several of these species have very limited distributions, and state-owned and private protected areas include species that are almost entirely restricted to such those areas (>85% of ESH). Unfortunately, human-driven habitat change has impacted significantly some species; e.g., ESH of *Anolis proboscis* in private protected areas is less than 50% of its ESH, and ESH of *Emmocliophis miops* in private protected areas is estimated to be around 1% of its ESH.
5.4 Discussion

Available biodiversity data for tropical regions, at all levels, is poor and far less robust than for temperate zones (Collen et al., 2008). A significant and continued investment is needed to establish and maintain systematic biodiversity monitoring programmes in these countries to generate reliable information for a better understanding of the situation and to contribute to conservation strategies and actions. Thus, monitoring programmes need to include all levels of biodiversity (genes, species, ecosystems), have comprehensive geographical and temporal scales and be scientifically rigorous and sensitive enough to detect meaningful changes (Mace and Baillie, 2007; Walpole et al., 2009; Butchart et al. 2010). Meanwhile, they need to be cost-effective and contribute to progress in more rapid ways than current programmes.

Despite significant conservation efforts, biodiversity has continued declining over the past two centuries, and there is no indication of a significant reduction of pressures from habitat change globally, and regional progress has been limited (Secretariat CBD, 2010, Balmford et al., 2005; Secretariat CBD, 2006, 2010; Walpole et al., 2009; Butchart et al. 2010). There is substantial reduction of intact habitats, and in 2016, only 23% of the global terrestrial areas are considered to have little or no human-mediated alterations (Watson et al., 2016). However, it is evident that the level of certainty of several indicators used to evaluate the impact of habitat change on biodiversity is heterogeneous, and most of them have grave gaps in terms of geographic, temporal or taxonomic coverage (Secretariat CBD, 2006, 2010; Walpole et al., 2009; Butchart et al. 2010). Information on the trends of habitat change is incomplete, large groups of organisms (including large clades of plants, vertebrates and invertebrates) have not been included in evaluations of the status of threatened species, trends in abundance and distribution are lacking for most species, and significant data is missing from before 1980 and after 2005 (Butchart et al. 2010; Secretariat CBD, 2010). Knowledge about
amphibians has progressively increased since the late 20th century, especially after the development of the Global Amphibian Assessment developed by the International Union of the Conservation of Nature IUCN (Gallant et al., 2007; Hoffmann et al., 2010; Oliveira et al., 2017; Stuart et al., 2004). However, knowledge about squamate reptiles is still disparate and limited (Bland and Böhm, 2016; Böhm et al., 2013; Gibbon et al., 2000; McCain, 2010; Pincheira-Donoso et al., 2013).

This chapter assessed the impact of human-driven habitat changes on the amphibians and reptiles of north-western South America. I generated evaluations using data from 914 species of amphibians and 564 species of reptiles, constituting the largest evaluation of habitat change impact for the region to date. Analyses were presented qualitatively and quantitatively at the level of taxonomic clades, biogeographic regions, ecological guilds (between forest and non-forest species), and IUCN extinction risk categories. The study provides crucial information for the evaluation of spatial patterns of habitat change impacts on Neotropical vertebrates and to the understanding of in-situ conservation management in Ecuador and Colombia.

Although amphibians and reptiles are usually referred to as part of a single group called “herpetofauna”, they have clear evolutionary, ecological and biogeographic differences (Duellman and Trueb, 1994; Vitt and Caldwell, 2013). Therefore, it is not surprising that they show different spatial characteristics, with amphibians having smaller more restricted distributions than reptiles, highly influenced by climate and geography (see Chapter 3). Species with more limited distributions are usually restricted to very specific environmental conditions due to ecophysiological adaptations and evolutionary history (Lomolino et al., 2016). However, species with more limited distribution have also been identified as more sensitive to impacts leading to greater population loss and decline of range size (Mace et al., 2008). Results presented herein support these conclusions for amphibians and reptiles.
Since distributional data is sometimes the strongest data available to evaluate the conservation status and extinction risks of many species, The IUCN Red List relies heavily on criteria related to species’ spatial attributes (Böhm et al., 2013; Hoffmann et al., 2010; Schipper et al., 2008; Stuart et al., 2004). Qualitative and quantitative analyses presented herein provide support for IUCN evaluations of threatened species of amphibians and reptiles, showing consistent high impacts by human-driven habitat changes in species classified under high extinction risk categories. The usefulness of this methodologies were also detected in studies focusing on global status of mammals and amphibians (Ficetola et al., 2015; Rondinini et al., 2011). However, those studies focused on habitat suitability instead of impact of habitat change. Most interestingly are the patterns comparing the different trends that threatened and non-threatened species exhibit to the impacts of habitat change. There was a direct relationship between the size of the distribution range of threatened species of amphibians and reptiles and the proportion of their range affected by habitat changes. Threatened species with larger ranges had larger amount of their range affected by habitat change. However, the pattern was inverse for non-threatened species, with species with larger ranges showing the least amount of habitat change impact.

Data deficient species are conservation conundrums (Bland and Böhm, 2016). These species lack quality data for evaluation of their conservation status and extinction risk (IUCN, 2017). In some cases, the problem with Data Deficient species is with the quality of available data, which does not allow to make an accurate evaluation. However, most Neotropical vertebrate species in this category are usually unknown beyond their taxonomic name, usually collected many decades ago without any further record, known only from few specimens—if not just the type series (Bland and Böhm, 2016; Butchart and Bird, 2010; Howard and Bickford, 2014; IUCN, 2016). Although data deficient category is in fact an informative classification (indicating the need for more information on those species), it has been found that species in that category are largely neglected in conservation strategies (Bland and Böhm, 2016;
Butchart and Bird, 2010; Howard and Bickford, 2014). In the absence of direct data for these species, methods to infer their conservation status and extinction risk have been proposed. Herein I used the method used by Ficetola et al. (2015) to identify several species of amphibians and reptiles that probably are better classified under threatened categories rather than as data deficient. This preliminary list should provide guidelines for researchers working on the amphibians and reptiles of north-western South America. In most cases, these species have not been recorded despite recent fieldwork, thus suggesting that they are rare, range-restricted, and most probably threatened. However, taxonomic uncertainty is also prevalent in some of these species, and urgent taxonomic work is urgently needed, especially in the genera *Colostethus*, *Hyloxalus*, *Pristimantis* and *Atractus* of Colombia, which are known to be taxonomically difficult (Arteaga et al., 2017; Brito et al., 2017; Grant et al., 2006).

Ecological differences between species are important determinants of their responses to habitat change. Although some non-threatened species reach high levels of habitat change (i.e., high reduction between ESH$_0$ and ESH$_H$), they correspond to non-forest amphibians that are adapted to anthropic environments, e.g., *Dendropsophus columbianus*, which inhabit pastures in areas formerly covered by cloud forest on the Cordillera Occidental of Colombia (Isaacs Cubides and Urbina-Cardona, n.d.), or *Gastrotheca ruizi* which, despite its small ESH$_H$, is well adapted to agricultural areas and fragments of riparian vegetation (Villota and Duellman, 2012). Actually, effects of human-driven habitat change on species that are habitat-generalists may be positive, allowing them to increase their populations or expand their geographic range (see Chapter 6).

I found strong biogeographic variation on the impacts by human-driven habitat change between the three biogeographic regions (Trans-Andean, Cis-Andean and High Andean regions) and ten biogeographic provinces that compose north-western South America (see Chapter 3). However, due to the biased distribution of protected areas, certain biogeographic regions and
provinces have suffered from higher impacts of habitat change, and their biodiversity is at higher extinction risk. While most of the highlands of the Andes have been extensively affected by habitat change, the Pacific lowlands still preserve large tracks of forested ecosystems and should be protected (Cuesta et al., 2017; Forero-Medina and Joppa, 2010). Protected areas are important for mitigation of habitat changes. State-owned protected areas are more efficient than private protected areas to mitigate the impact of human-driven habitat change at large scales, although habitat loss towards their borders is sometimes inevitable. Despite private protected areas being smaller, they are particularly substantial to the preservation of small areas of high biodiversity value, although they are vulnerable to external fragmentation and isolation (Langholz and Lassoie, 2001; Langholz et al., 2000). Results from this study coincides with other studies that have provided strong evidence for the importance of in-situ conservation strategies and its application in priority areas for biodiversity conservation (e.g., Cuesta et al., 2017; Forero-Medina and Joppa, 2010; Sierra et al., 2002)
References


Appendices

Appendix 1 Amphibians with ESH coinciding exclusively with state-owned or private protected areas

<table>
<thead>
<tr>
<th>State-owned protected areas</th>
<th>Private protected areas</th>
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<tr>
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<tr>
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</tr>
<tr>
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<tr>
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Appendix 2 Squamate reptiles with ESH coinciding exclusively with state-owned or private protected areas

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<td><em>Trilepida dugandi</em></td>
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Appendix 3. Map showing species richness of amphibians of north-western South America, human-driven habitat-change, and borders of protected areas

Map showing species richness of amphibians of north-western South America (from green to red), human-driven habitat-change (white areas inside Ecuador and Colombia), and borders of protected areas (black).
Appendix 4. Map showing species richness of squamate reptiles of north-western South America, human-driven habitat-change and borders of protected areas

Map showing species richness of squamate reptiles of north-western South America (from green to red), human-driven habitat-change (white areas inside Ecuador and Colombia), and borders of protected areas (black).
Chapter 6  Habitat changes as mediators of natural colonisations and invasions by amphibians, reptiles and birds: Study case of the Galapagos Islands
6.1 Introduction

Extra-range dispersal is a natural process that has been fundamental to the development of biogeographic patterns throughout Earth’s history (Wilson et al. 2009). Individuals moving to new areas usually confront a different set of biotic and abiotic variables, and most dispersed do not survive. However, if they are able to survive and adapt to the new conditions, they may establish self-sufficient populations, colonise the new area and even spread into nearby locations. (Mack et al. 2000). In doing so, they will produce ecological transformations in the new areas, which may lead to changes in other species’ populations, communities and speciation, as well as the formation of new ecosystems (Wilson et al. 2009). Human extra-range dispersals since the Pleistocene have produced important distribution changes in species of all taxonomic groups. Throughout our prehistory and history, we have aided other species’ extra-range dispersals either by deliberate translocations or by ecological facilitation due to habitat changes or modifications of ecological relationships (Boivin et al. 2016). Over the last few centuries, human globalisation has led to the integration of most areas of the planet. Due to advances in transportation, humans and their shipments travel faster and further than ever before. Unintentionally or deliberately, thousands of species of flora, fauna and microorganisms have been translocated and introduced to places that they would not have reached on their own and that are beyond the biogeographic barriers that previously prevented their spread in such a timeframe (Ricciardi 2007). However, most translocated species (especially those that are unintentionally introduced) are already adapted to anthropogenic niches in the new places in which they find themselves. Given

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20 I have published part of this chapter in the book chapter “The Hitchhiker Wave: Non-native Small Terrestrial Vertebrates in the Galapagos” published as part of the book “Understanding Invasive Species in the Galapagos Islands” by Elsevier (Cisneros-Heredia 2018).
that the areas to which they arrive are usually also under anthropogenic impact, their adaptation process and possibility of survival are increased.

Non-native species contribute to the homogenization Earth’s biota, but ongoing scientific debates on the processes, effects, importance and management of non-native species are intense (David 2003; Brown & Sax 2004, 2005; Cassey et al. 2004; Dukes & Mooney 2004; Davis et al. 2011; Chew & Carroll 2011; Ricciardi et al. 2013; Simberloff et al. 2013; Chew 2015; Kuebbing & Simberloff 2015; Pereyra 2016; Sol 2016). Non-native species may modify biological communities and ecosystem functions by becoming, for example, predators, competitors, preys, seed dispersers, parasites, disease vectors or ecosystem engineers (Daszak et al. 2000; Mooney & Cleland 2001; Crooks 2002; O’Dowd et al. 2003; Doddy et al. 2009; Capps & Flecker 2013; Ricciardi et al. 2013; Simberloff et al. 2013). Non-native species may also have economic, social, cultural and health impacts on human populations (Vitousek et al. 1997; Pejcher & Mooney 2009). Non-native species that are successful and disperse further in their new areas become invasive and have been reported as major anthropogenic drivers of current changes in biodiversity (Vitousek et al. 1997; Chapin III et al 2000; Mace et al. 2005; Clavero & Garcia-Berthou 2005; Belard et al. 2016; Doherty et al. 2016). However, evidence, scientific perspectives and practical implications for this assertion are still under examination (Gurevitch & Padilla 2004a,b; Ricciardi 2004; Didham et al. 2005; MacDougall & Turkington 2005; Young & Larson 2011; Russell & Blackburn 2017).

Extra-range expansions involving native and non-native vertebrates have been reported in north-western South America (Aguilar et al., 2016; Cisneros-Heredia, 2004; Cisneros-Heredia et al., 2015; Crespo-Pérez et al., 2016; Olmstead et al., 2011). However, most available information is based on isolated records dispersed across the entire region, without enough data on geographic or temporal patterns, or impacts. In spatially restricted ecosystems, such as island and wetlands, the effects of invasive non-native species on native biodiversity can be severe and lead to extensive
transformation of native ecosystems and even to the extinction of endemic species (David 2003; O'Dowd et al. 2003; Blackburn et al. 2004; Mace et al. 2005; Simberloff et al. 2013). While most of this dissertation has studied the biodiversity of mainland north-western South America, the Galapagos Islands (herein referred to simply as “Galapagos”) are of particular interest and relevance to the issue of species introduction and invasiveness, and are the perfect scenario for analyses of habitat change as mediator of range expansion of species.

The human population in Galapagos has increased significantly over the past few decades, and transportation links carrying local travellers, tourists and supplies have facilitated the arrival of non-native species (Mauchamp 1997; Causton et al. 2006; Tye 2006; González et al. 2008; Phillips et al. 2012). Invasive non-native species have been identified as the principal threat to biodiversity in the Galapagos terrestrial ecosystems (Causton et al. 2006). For example, feral populations of Dogs *Canis familiaris*, Cats *Felis catus* and Pigs *Sus scrofa* as well as Black Rats *Rattus rattus* have been reported to predate on several endemic species, causing serious declines in the populations of Galapagos Tortoises *Chelonoidis* spp., Galapagos Land Iguanas *Conolophus subcristatus*, Marine Iguanas *Amblyrhynchus cristatus* and Galapagos Penguins *Spheniscus mendiculus*, among others (Konecny 1987; Phillips et al. 2012). Grazing and trampling by feral Goat *Capra hircus* have depleted the populations of several native and endemic plants, including the critically endangered Santiago Scalesia *Scalesia atractyloides* and Floreana Flax *Linum cratericola*, which are now on the verge of extinction (Schofield 1989; Aldaz et al. 1997; Simbaña & Tye 2009). Feral Cattle *Bos taurus* aided the spread of the invasive Common Guava *Psidium guajava* and non-native grasses by habitat engineering and seed dispersing (Phillips et al. 2012). The parasitic fly *Philornis downsi* is causing significant excess mortality amongst the endemic and threatened Darwin’s Medium Tree Finch *Camarhynchus puper* (O’Connor et al. 2010). Cottony-Cushion Scale *Icerya purchasi* has become a pest causing population declines in the endemic Thin-leafed Darwin’s Shrub *Darwiniothamnus*
Ambitious programmes to control and eradicate non-native species have been established in the archipelago (e.g., Barnett 1986; Campbell et al. 2004; Cruz et al. 2005; Carrión et al. 2007). However, ecological interactions are of a complex nature and invasive species may, in some cases, contribute to the maintenance of ecosystem functions in those systems that are experiencing environmental change (Buckley and Catford 2016). For example, Black Rats have become a seed disperser of the endemic *Miconia robinsoniana* in some agricultural areas of San Cristobal Island (Riofrío-Lazo and Páez-Rosas 2015). Black Rats have also become the most important prey for Galapagos Hawk *Buteo galapagoensis* since the eradication of feral Goats in Santiago Island (Jaramillo et al. 2016). Non-native species may also help manage invasive species, acting as biological controls. For example, the Vedalia Beetle *Rodolia cardinalis* was deliberately introduced to Galapagos to control the spread of the Cottony-Cushion Scale *I. purchasi* (Calderón-Álvarez et al. 2012).

In the most recent comprehensive review on non-native vertebrates living in Galapagos, Phillips et al. (2012) pointed out that vertebrate introductions in Galapagos are shifting away from intentionally introduced species, such as domestic mammals, towards hitchhiking species, such as reptiles (Phillips et al. 2012). Furthermore, the authors remarked that snakes and lizards (i.e., squamate reptiles) could pose the greatest threat to Galapagos biodiversity in the future. An unfortunately accurate prediction, while Phillips and collaborators were writing their article, the Common House Gecko *Hemidactylus frenatus*, a lizard profiled as highly invasive, had already arrived in Galapagos (Torres-Carvajal & Tapia 2011).

Despite that only six years have passed since Phillips et al. (2012) published their study, the panorama of non-native terrestrial vertebrates in Galapagos has changed in important ways, in particular for non-mammals. Although several studies have dealt with the impacts and management of non-native
species in Galapagos, nothing has been said about the relationship between the establishment of non-native species and anthropogenic habitat changes in the islands. Since hitchhiker species are usually species already adapted to anthropogenic areas, this discussion is certainly important. Thus, in this paper, I analyse the importance of habitat change as a factor that facilitates the establishment of non-native species. This study is based on information about the current status, invasiveness and potential impact of all non-native amphibians, reptiles and birds that have been reported in the Galapagos Islands.

6.2 Methodology

6.2.1 Study area

The Galapagos Archipelago is a group of volcanic marine islands located in the eastern Pacific Ocean, separated from the nearest mainland (the coast of Ecuador) by ca. 930 km. Nineteen main islands (> 1 km²) and over 100 islets and rocks constitute the archipelago, totaling ca. 7850 km² of land, spread out over ca. 430 km (straight line between the outermost islands: Darwin and Española). The largest islands are Isabela (4588 km²), Santa Cruz (986 km²), Fernandina (642 km²), Santiago (585 km²), San Cristobal (558 km²), Floreana (173 km²) and Marchena (130 km²) (Snell et al. 1996).

The climate of Galapagos largely depends on the oceanic currents and winds, resulting in vegetation distribution being determined by orogenic rainfall (Jackson 1993; Wiggins & Porter 1971). On the lowlands, all islands and islets are arid and warm. A narrow belt along coastal areas, called Littoral Zone\textsuperscript{21}, is dominated by salt-tolerant shrubs and small trees. Xerophytic low scrub, arborescent and shrubby cacti, and thorn woodland and deciduous forest are the main vegetation in the lowlands (i.e., Dry Zone\textsuperscript{1}). A Transition Zone\textsuperscript{1} with

\textsuperscript{21} Ecological classification of vegetation based on the proposal by Wiggins & Porter (1971).
taller trees, denser canopy, and more mesic conditions than the Dry Zone appears with increasing elevation (here plants represent a mix from lower and higher zones). Moist conditions exist in the islands above 300–600 m, where three vegetation zones have been recognised: Humid Zone\(^1\), with incremented humidity and denser vegetation dominated by evergreen species, in particular the endemic Giant Daisy Tree, genus *Scalesia*; Very Humid Zone, with very dense vegetation dominated by the endemic Galapagos Miconia *Miconia robinsoniana*; and Pampa Zone, tree-less and dominated by sedges and ferns above regional treeline. An Upper Dry Zone\(^1\)—a climatic inversion zone with drier conditions, exists on Cerro Azul and Wolf volcanoes, which reach beyond 1000 m above the main cloud layer. This zone is covered by scrub vegetation dominated by *Opuntia* cacti or *Scalesia*. On the leeward side of islands, the Littoral, Dry and Transition zones rise higher and the moister zones may be absent (Wiggins & Porter 1971). The moist zones (Humid, Very Humid, and Pampa) are only present on the largest islands (i.e., Santa Cruz, San Cristobal, Pinta, Santiago, Floreana, Isabela and Fernandina). In addition to these natural ecosystems, humans have modified large sections of the Dry, Transition, Humid and Very Humid zones on the four inhabited islands, transforming them into agro-urban areas dominated by large populations of non-native plant species (Wiggins & Porter 1971; Guézou et al. 2010). The Pampa Zone has been enlarged by human activities and grazing by non-native mammals.

World famous for their biodiversity and role in the formulation of the theory of evolution by natural selection, Galapagos are home to a vast array of endemic species of flora and fauna. Galapagos biodiversity evolved in isolation from its continental counterparts. Moreover, its uniqueness is not just due to differences between insular and continental species, but also due to a large level of inter-insular endemism. There are many taxa restricted to just one or few islands (Parent and Crespi 2006; Sequeira et al. 2008; Benavides et al. 2009; Hoeck et al. 2010; Poulakakis et al. 2012; Torres-Carvajal et al. 2014; MacLeod et al. 2015; Carmi et al. 2016). The Galapagos Archipelago is home
to no less than 211 terrestrial vertebrates, including: six endemic species of snakes of the genus *Pseudalsophis*, 24 endemic lizards (genus *Phylodactylus, Amblyrhynchus, Conolophus, Microlophus*), 12 endemic giant tortoises of the genus *Chelonoidis*, 160 species of birds (of which 46 taxa are endemic) and nine species of mammals (of which 7 taxa are endemic).

The Galapagos Islands are among the few Pacific islands that were not settled by aboriginal humans (Anderson et al. 2016). The first settlement was established in 1832, although pirate and whaling ships frequently visited the archipelago beginning in the 16th century. Currently, Santa Cruz, San Cristobal, Isabela and Floreana islands have human populations established in the lowlands and highlands. The towns on each island are as follows (in parenthesis, population and growth rate between 2010–2015; INEC, 2015):

- **Santa Cruz Island**: Puerto Ayora (11822, 1.4%), Bellavista (3384, 7.0%), Santa Rosa (495, -2.7%).
- **San Cristobal Island**: Puerto Baquerizo Moreno (6553, 1.3%), El Progreso (535, -4.0%).
- **Isabela Island**: Puerto Villamil (2164, 1.6%), Tomás de Berlanga (180, 1.9%).
- **Floreana**: Puerto Velasco Ibarra (111, -4.1%).

There are airports in San Cristobal, Isabela and Baltra islands, with connections to Guayaquil and Tababela (Quito) airports in mainland Ecuador. All populated islands have maritime ports for passengers and freight, with connections to several international and national ports, including the Ecuadorian ports of Guayaquil, Manta and Salinas (Cruz-Martínez et al. 2007).

### 6.2.2 Data collection

I processed information for all species of amphibians, reptiles and birds recorded in terrestrial and freshwater environments in the Galapagos Islands based on data from my own surveys, examination of specimens in museums
collections, literature review, photographic identification based on images available on the internet with confirmed locality data, and critical analyses of global databases (eBird and GBIF). Seabirds and migratory birds were not included in this study.

I conducted fieldwork in San Cristobal Island, Galapagos, in June 2005, June–August 2009, June–August 2010, July–August 2011, July 2013, June 2016 and June–July 2017. Surveys were conducted in urban, agricultural and natural areas. I searched for vertebrate fauna through time-limited visual encounter surveys. I also looked for dead-on-road (DOR) animals. No specimens were collected.

I examined specimens of amphibians, reptiles and birds deposited at seven museums: División de Herpetología, Museo de Ciencias Naturales del Instituto Nacional de Biodiversidad, Quito (DHMECN); Fundación Herpetológica Hustavo Orcés, Quito (FHGO); Museum of Natural History, University of Kansas, Lawrence (KU); The Natural History Museum, London (BMNH); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ); Universidad San Francisco de Quito, Quito (DFCH-USFQ); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Museo de Zoología de Vertebrados and Universidad del Azuay, Cuenca (ZOOA). Voucher specimens in collections were either borrowed and examined by me to verify species identification or verified by curatorial staff within their respective institutions. Although museum databases are available online (e.g., GBIF), I avoid including data from specimens whose identifications I was unable to confirm.

Published geographic information was synthesised based on a literature review using the library systems of King’s College London and Universidad San Francisco de Quito USFQ, Google Scholar™ scholarly texts search (https://scholar.google.com) and the Biodiversity Heritage Library (http://www.biodiversitylibrary.org). Relevant references were gathered
using search terms consisting of “Key terms AND Galapagos”, in which key terms corresponded to scientific and common names data at the class, family, genus and species levels (including synonyms, previous taxonomic classification and alternative orthographies).

For species with diagnostic colouration patterns and morphology that allow their unambiguous identification in photographs, I assembled data from photographic vouchers in the search engines of Flickr™ (https://www.flickr.com, by Yahoo!), iNaturalist.org™ (http://www.inaturalist.org, by California Academy of Sciences) and Google Images™ search service (https://images.google.com, by Google, Inc.). Relevant images were gathered using search terms consisting of “Genus AND Species” or “Common name” where Genus and species or Common name were replaced by the corresponding data for each species (including synonyms, previous taxonomies and different orthographies).

Georeferenced data from Flickr and iNaturalist were automatically added to GeoCat (Bachman et al. 2011; http://geocat.kew.org) and then imported to Google Earth™ mapping service (7.1.5.1557 release by Google, Inc. on May 2015). All other localities, gathered from literature, museum or photographic records, were georeferenced manually in Google Earth based on direct information (coordinates and altitudinal data) when available. Additional data (including catalogue and field notes) relevant to obtaining accurate and precise positioning was collected, following recommendations by Wieczorek et al. (2004) was used. All localities were reviewed and validated individually, and coordinates were amended when incorrectly georeferenced in the source. I determined the position most closely related to the locality description using toponymic information based on the Geographic Names Database, containing official standard names approved by the United States Board on Geographic Names and maintained by the National Geospatial-Intelligence Agency (http://geonames.nga.mil/gns/html/), OpenMapStreet data available under
the Open Database Licence (http://www.openstreetmap.org), and gazetteers for Ecuador (Brown 1941, Peters 1955, Lynch and Duellman 1997).

6.2.3 Data analysis

6.2.3.1 Species Definitions
Because the focus of this study was to determine the function of inland habitat changes as mediators of natural colonisations and invasions, I included data only for dispersing species. Dispersing species are herein defined as those undergoing extra-range dispersals, defined as the movement of propagules of a species from their current range to a new area beyond the boundaries of their range occupied over ecological timescales (Wilson et al. 2009). All native species are excluded from the analyses (see definitions below).

When studying extra-range dispersals, the dichotomy of native/non-native species is a predominant concept in ecology, biogeography and conservation biology (Mace et al. 2005; Lomolino et al. 2010; Simberloff et al. 2013). It has been widely adopted in analysis of the conservation of Ecuadorian biodiversity and particularly in Galapagos (Josse 2001; Causton et al. 2006). However, a dichotomous approach is evidently simplistic and even artificial in complex and dynamic systems. The cornerstone term “native species” is part of an ongoing scientific and philosophical debate about its conceptual and operational definitions as well as its relevance and applicability in ecological, conservation, management, sociocultural and economic activities (Chew and Hamilton 2011, Clavero 2014, Van Der Wal et al. 2015).

A dichotomous native/non-native approach is hard to make fully operational in regions where it is difficult to assess the status of an archaeophyte/archaeozoan versus a native taxon, or where the distinction between native and non-native taxa is not absolute (Preston et al. 2004). However, these issues are greatly controlled in Galapagos, due to the isolation of the archipelago and the specific date related to human arrival. Although recognising issues associated with a dichotomous approach, I—for the sake of
operational straightforwardness and due to the particular nature of Galapagos
geography and history—use the following working definitions (modified
from Pyšek et al. 2009):

*Native taxa* are those that originated in a given area or that arrived through
extra-range dispersal from an area in which they are native by their own
means. Their successful arrival is due to their adaptation for dispersal and
survival in the physiological and ecological conditions across the dispersal
routes, which do not act as strict dispersal barriers. Complete or partial
synonyms include terms like “indigenous” or “autochthonous taxa”.

*Non-native taxa* are those that have arrived from an area in which they are non-
native or that arrived through extra-range dispersal from their native range
by extrinsic dispersal mechanisms (i.e., outside of their own natural dispersal
potential). These extrinsic mechanisms provide specific conditions that allow
these taxa to disperse across environments that otherwise would be severe
natural barriers in the same timeframe. Complete or partial synonyms include
terms like “alien”, “exotic”, “non-indigenous” or “allochthonous taxa”.

It is worth noting that dispersing species can be both native and non-native
taxa. Extra-range dispersals that involve native species are usually perceived
as only happening over long, evolutionary timescales, but they actually may
overcome in shorter ecological timescales.

Human intervention was intentionally left out of this analysis in order to
establish working definitions on the basis of ecological and biogeographic
criteria only. Human extra-range dispersals do facilitate the arrival of non-
native taxa via direct or indirect extrinsic mechanisms. Nevertheless, natural
extra-range dispersals and those mediated by humans are similar ecological
processes (Buckley and Catford 2016; Hoffmann and Courchamp 2016).
However, management decisions usually require more straightforward
answers, which although taking into account the complex and chaotic reality
of natural systems, provide solutions that can be efficiently understood and
applied. The geographical origin of species should not be used as the only criteria guiding management and control decisions (Buckley and Catford 2016; Hoffmann and Courchamp 2016), but rather a distinction between natural and human-mediated extra range dispersals is at least partially necessary when management and control issues are involved. For example, if a species reached a new area by its own means and without the intervention of an extrinsic dispersal mechanisms (including without human intervention), it would most probably be able to do so repeatedly as it is evidenced that the species has the capability to disperse across natural barriers that separated its geographical origin and new areas. Any proposed regulations to control its population would be insufficient and inefficient as new specimens would most certainly continue to arrive. On the other hand, a non-native species that solely depends on human-mediated extrinsic dispersal mechanisms could be controlled by regulating the aforesaid mechanisms. Therefore, natural extra-range dispersals (i.e., where human mediation is not involved) are herein called natural colonisations, while human-mediated extra-range dispersals are called introductions.

By applying all aforementioned definitions, the following statements can be made about Galapagos biodiversity:

- Since Galapagos was not settled by aboriginal humans (Anderson et al. 2016), the first human activities and the movement of dispersing species started with the European discovery of Galapagos in 1535 (Peck et al. 1998). Therefore, all species that were established in Galapagos before 1535 apparently arrived on the island during evolutionary timescales and are considered [non-dispersing] native species.

- Species that reached the archipelago through their own means after 1535 due to their own successful oceanic dispersal capacities (and probably due to several dispersal events) and that have established populations by natural colonisation are considered dispersing
native species.

- Species that reached the archipelago after 1535 through extra-range dispersal by extrinsic dispersal mechanisms are dispersing non-native species. Due to the long distance between Galapagos and mainland (and even other islands), all dispersing non-native species seem to have arrived due to intentional or unintentional introductions.

6.2.3.2 Categories of residency and establishment

Each dispersing species was assigned to one of the following residency categories:

- **Resident**, for species that have been able to establish breeding populations in any of the islands of the Galapagos Archipelago.
- **Eradicated**, for species that were able to establish breeding populations but were subsequently eradicated by natural or human-mediated processes.
- **Regular vagrant**, for nonbreeding visitors with no established pattern of occurrence, records in three or more islands and/or with more than ten records in the archipelago over the last 35 years.
- **Irregular vagrants**, for nonbreeding visitors with no established pattern of occurrence, records in two or one island and/or with less than ten records in the archipelago over the last 35 years.

Migrants were distinguished from vagrants as having an established pattern of seasonal occurrence and usually breeding in the northern hemisphere. The 35-year threshold was chosen to lower the effects of El Niño Southern Oscillation (ENSO) events on atypical extra-range dispersal (Curry & Stoleson 1988; England 2000; Jaksic & Fariña 2010). This period encompasses the three strongest ENSO events since 1950: 1982–1983, 1997–1998, and 2015–2016 (NOAA 2017).
In any environment, there is an introduction-invasion continuum between the arrival of non-native species, their establishment and their shift into an invasive species (Mack et al. 2000; Blackburn et al. 2011; Pereyra 2016). Dispersing species introduced to Galapagos are heterogeneous in terms of their establishment, spread, dominance and impact. Only a fraction of the dispersing species that arrive does become resident and an even smaller portion is able to establish spreading populations. For example, out of 754 non-native vascular plants recorded by Guézou et al. (2010) in the inhabited areas of Galapagos, 35% have established populations; and Tye et al. (2002) classified 5% of those species as invasive. As for insects, 463 non-native species were reported by Causton et al. (2006) in Galapagos, with at least 73% of them having established populations and 13% of species being classified as invasive.

In order to provide a straightforward evaluation of the degree of establishment of dispersing amphibians, reptiles and birds in Galapagos—-independent of their conservation-related effects—I adopted the categories proposed by McGeoch and Latombe (2016), with some modifications (Table 5). This typology is based on three main factors: degree of expansion, population size and time since arrival (McGeoch and Latombe 2016). Since all dispersing species arrived to Galapagos within the last two centuries, all could be classified as recent. However, I differentiate between historic (the last two centuries) and recent (the last decades) translocations. Additionally, I take into account the fact that introductions have not been synchronised and that some dispersing populations are the result of more than one introduction event.
Table 5. Topology to evaluate the degree of residency and establishment of dispersing amphibians, reptiles and birds in Galapagos

Topology to evaluate the degree of residency and establishment of dispersing amphibians, reptiles and birds in Galapagos, independent of their conservation effects. This table is based on McGeoch and Latombe (2016), with some modifications.

<table>
<thead>
<tr>
<th>Residency</th>
<th>Establishment</th>
<th>Degree of expansion</th>
<th>Population size</th>
<th>Time since establishment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irregular vagrant</td>
<td>Non-established</td>
<td>Intercepted</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>Irregular vagrant</td>
<td>Non-established</td>
<td>Narrow</td>
<td>None</td>
<td>Recent/Historic</td>
</tr>
<tr>
<td>Regular vagrant</td>
<td>Non-established</td>
<td>Wide</td>
<td>None</td>
<td>Recent/Historic</td>
</tr>
<tr>
<td>Resident</td>
<td>Domestic</td>
<td>Human-dependant</td>
<td>Human-dependant</td>
<td>Recent/Historic</td>
</tr>
<tr>
<td>Resident</td>
<td>Newly established</td>
<td>Narrow</td>
<td>Small</td>
<td>Recent</td>
</tr>
<tr>
<td>Resident</td>
<td>Incipient</td>
<td>Narrow</td>
<td>Large</td>
<td>Recent</td>
</tr>
<tr>
<td>Resident</td>
<td>Dispersed</td>
<td>Wide</td>
<td>Small</td>
<td>Recent</td>
</tr>
<tr>
<td>Resident</td>
<td>Successful</td>
<td>Wide</td>
<td>Large</td>
<td>Recent</td>
</tr>
<tr>
<td>Eradicated</td>
<td>Eradicated</td>
<td>Wide/Narrow</td>
<td>None</td>
<td>Recent/Historic</td>
</tr>
<tr>
<td>Resident</td>
<td>Uncommon</td>
<td>Narrow</td>
<td>Small</td>
<td>Historic</td>
</tr>
<tr>
<td>Resident</td>
<td>Constrained</td>
<td>Narrow</td>
<td>Large</td>
<td>Historic</td>
</tr>
<tr>
<td>Resident</td>
<td>Sparse</td>
<td>Wide</td>
<td>Small</td>
<td>Historic</td>
</tr>
<tr>
<td>Resident</td>
<td>Highly Successful</td>
<td>Wide</td>
<td>Large</td>
<td>Historic</td>
</tr>
</tbody>
</table>

6.2.3.3 Arrival pathways

To evaluate the pathways of arrival of dispersing species, I adopted the simplified framework proposed by Hulme et al. (2008), with some modifications (
Table 6). This framework was designed for “biological invasions”, but it is herein applied to all dispersing species, independently of their native/non-native statuses or the degrees to which they have become successfully established in the new environment.
Table 6. **Simplified framework to categorise pathways of initial introduction of dispersing species amphibians, reptiles and birds in Galapagos**

Simplified framework to categorise pathways of initial introduction of dispersing species amphibians, reptiles and birds in Galapagos, independent of their conservation effects. This table is based on Hulme et al. (2008) with some modifications.

<table>
<thead>
<tr>
<th>Introduction mechanism</th>
<th>Pathway</th>
<th>Human intervention</th>
</tr>
</thead>
<tbody>
<tr>
<td>Importation of commodity</td>
<td>Pet/Domestic</td>
<td>Intentional</td>
</tr>
<tr>
<td>Importation of commodity</td>
<td>Release</td>
<td>Intentional</td>
</tr>
<tr>
<td>Importation of commodity</td>
<td>Escape</td>
<td>Intentional</td>
</tr>
<tr>
<td>Importation of commodity</td>
<td>Contaminant</td>
<td>Unintentional</td>
</tr>
<tr>
<td>Transport vector</td>
<td>Hitchhiker</td>
<td>Unintentional</td>
</tr>
<tr>
<td>Dispersal from neighbouring region</td>
<td>Corridor</td>
<td>Unintentional</td>
</tr>
<tr>
<td>Dispersal from neighbouring region</td>
<td>Unaided</td>
<td>No intervention</td>
</tr>
</tbody>
</table>

6.2.3.4 **Identification of potential hitchhikers**

Hitchhikers are dispersing species that are carried or transported by chance or unintentionally attached to or within transport vectors. Hitchhiker species are directly associated with human transport, may arrive via one or more vectors (e.g., maritime or air transportation) and are independent of a specific commodity (Hulme et al. 2008). A synonymous term is “stowaway species”.

There is not a single set of characteristics that determine the potential of vertebrates to become successful hitchhikers or to become established in insular ecosystems. Several publications have reviewed and proposed different methods for predicting introduced species. Since I am analysing three different phylogenetically diverse groups of terrestrial vertebrates, I will use basic criteria for each group, which I selected after studying the following references: Kolar and Lodge (2001), Hayes and Barry (2008), Van Wilgen & Richardson (2012) and Buckley and Catford (2016). I think that this set of criteria allows a fast and simple identification of potential species in mainland Ecuador that could hitchhike to Galapagos.
6.2.3.5 Ecosystem categories

In order to identify how records of dispersing species were linked with habitat changes, I divided ecosystems according to the degree and type of human disruption into three broad ecosystem units: urban, agricultural and natural ecosystems. I gathered this data from the most updated map of Galapagos ecosystems (Rivas et al. 2016).

- *Natural* ecosystems, are biotic communities in conjunction with abiotic components interacting as systems in areas that have been shaped during evolutionary timescales and where human processes and activities have minor or no impact at the ecosystem level.

- *Human-modified* ecosystems are those in which human processes and activities have had significant impacts at the ecosystem level, and are divided into:

- *Urban* ecosystems, biotic communities in conjunction with abiotic components interacting as systems in urban spaces. For the sake of operational straightforwardness and due to the rather small population (111–11822 human inhabitants in 8 towns) and human geographic history in Galapagos, urban spaces, as herein defined, include both urban and suburban areas and may include peri-urban areas as long as there are no agricultural activities present in them (see Ravetz et al. 2013 for definitions of each specific area). Urban ecosystems are strongly shaped by human-made infrastructure and are the result of human-designed processes. Urban ecosystems encompass three different type of urban spaces: grey (e.g., buildings, roads), green (vegetation) and blue spaces (freshwater wetlands with visible water). All three types of spaces are highly diverse due to their geomorphological,
climatic, biological, historic and social conditions.

- Agricultural ecosystems, are biotic communities in conjunction with abiotic components interacting as systems in peri-urban and rural spaces where agricultural activities are developed (see Ravetz et al. 2013 for definitions of each specific area). Agricultural ecosystems are dedicated to the cultivation and breeding of biodiversity used to sustain and enhance human life (ILO 1999). Agricultural spaces are the result of human-designed processes, but human-made infrastructures are not predominant. Agricultural ecosystems encompass both active and non-active farmlands. For the sake of operational straightforwardness and since all invasive plant species have agricultural origins, spaces in which invasive species are predominant and have displayed natural ecosystems are also considered agricultural ecosystems (despite not having been created as the direct result of human-designed processes).

6.3 Results

6.3.1 Overview

I report herein a total of 39 dispersing species of amphibians (3 spp.), squamate reptiles (8 spp.), chelonians (3 spp.) and birds (25 spp.) in the Galapagos Archipelago, including 13 native and 26 non-native species (Appendix 1). Dispersing species are equivalent to 18% of all Galapagos amphibians, reptiles and birds. Subsequent analysis in this study will include only 30 species because: (i) Six dispersing species of birds occur in the Galapagos only in agro-urban areas under direct human care and have not

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22 Differences between the previous works of Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a) are explainable by: (i) a better understanding of some species’ status (for details, see species accounts in Appendixes 1, 2 and 3) and (ii) due to the arrival of new non-native vertebrates. The present study includes two species not reported in previous reviews.
established self-sustaining populations outside of farms, thus their presence is a direct consequence of human care and not affected by habitat changes; (ii) two species of birds and one tortoise have been reported in Galapagos but further confirmation beyond these reports is unavailable.

Santa Cruz (23 spp.), San Cristobal (18 spp.) and Isabela (16 spp.) are the islands with the largest amount of reported dispersing amphibians, reptiles and bird species. Six species have been reported in Floreana, five in Baltra and four in Genovesa. The islands of Marchena, Española, Santa Fe, Santiago, Fernandina, North Seymour, Rabida, Bartolome, Pinta, Pinzon and Champion Islet each have only one or two reported species (Appendix 1).

In general, human population growth in Galapagos is correlated with most variables of dispersing species richness, including when native/non-native or vagrant/resident species are analysed separately (Table 7). Only vagrant non-native species richness and resident native species richness are weakly correlated with human population growth (Table 7). On the contrary, most variables of dispersing species richness are weakly correlated with increasing tourism. This is true in all cases except for the accumulated richness of dispersing species, all vagrant species, vagrant non-native species and, to a lesser degree, vagrant native species and all non-native species.
Table 7. **Summary of Pearson’s coefficient of correlation (r²) between different variables related to dispersing species in Galapagos and human population growth**

Summary of Pearson’s coefficient of correlation (r²) between different variables related to dispersing species in Galapagos and human population growth (data from censuses of 1938, 1950, 1962, 1974, 1982, 1990, 1998, 2001, 2010, 2015) and the increasing number of tourists (years 1979–2015). Underlined values show weak correlations. The value in bold face is the only variable that was not correlated with growth of the human population or the number of tourists. Abbreviations: spp. = species; d.f. = degrees of freedom; P-values greater than 0.05 are marked as ns; P-values less than 0.01 with two asterisks (**); and P-values less than 0.001 with three asterisks (***)..

<table>
<thead>
<tr>
<th>Variables</th>
<th>r² with Human Population Growth (8 d.f.)</th>
<th>r² with Increasing Number of Tourists (35 d.f.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accumulated richness of dispersing spp.</td>
<td>r² = 0.91 ***</td>
<td>r² = 0.95 ***</td>
</tr>
<tr>
<td>Accumulated richness of vagrant spp.</td>
<td>r² = 0.97 ***</td>
<td>r² = 0.93 ***</td>
</tr>
<tr>
<td>Adjusted richness of vagrant spp.</td>
<td>r² = 0.74 ***</td>
<td>r² = 0.33 ***</td>
</tr>
<tr>
<td>Accumulated richness of vagrant non-native spp.</td>
<td>r² = 0.91 ***</td>
<td>r² = 0.95 ***</td>
</tr>
<tr>
<td>Adjusted richness of vagrant non-native spp.</td>
<td>r² = 0.67 **</td>
<td>r² = 0.49 ***</td>
</tr>
<tr>
<td>Accumulated richness of vagrant native spp.</td>
<td>r² = 0.88 ***</td>
<td>r² = 0.70 ***</td>
</tr>
<tr>
<td>Adjusted richness of vagrant native spp.</td>
<td>r² = 0.89 ***</td>
<td>r² = 0.40 ***</td>
</tr>
<tr>
<td>Accumulated richness of resident spp.</td>
<td>r² = 0.75 ***</td>
<td>r² = 0.42 ***</td>
</tr>
<tr>
<td>Accumulated richness of resident non-native spp.</td>
<td>r² = 0.83 ***</td>
<td>r² = 0.54 ***</td>
</tr>
<tr>
<td>Accumulated richness of resident native spp.</td>
<td>r² = 0.59 **</td>
<td>r² = 0.09 ns</td>
</tr>
<tr>
<td>Accumulated richness of native spp.</td>
<td>r² = 0.80 ***</td>
<td>r² = 0.40 ***</td>
</tr>
<tr>
<td>Accumulated richness of non-native spp.</td>
<td>r² = 0.80 ***</td>
<td>r² = 0.61 ***</td>
</tr>
</tbody>
</table>

Initially, only two resident dispersing species were established in Galapagos during more than 100 years. However, since the 1950’s the slope of the accumulation curve has rapidly increased and eight resident species were established by 1980. Since then, the rate of increase slowed and a total of 10 resident dispersing species had established self-sufficient populations in Galapagos by the 1990s. Subsequent increases in the establishment of new resident dispersing species has been lower, and only one additional species has established self-sufficient populations in Galapagos since the 1990s. The
pattern for vagrant dispersing species is less clear, but a significant surge is clearly observed after the late 1950s, which later became and since the 1990s, on average, 5–7 new species have been able to establish themselves every year (Figure 25).

Change of accumulated richness of dispersing species that have arrived to Galapagos in the 20th century, human population in Galapagos between 1938 and 2015 and the number of tourist per year (divided by 10) between 1979–2015. Dispersing species are separated into resident species and vagrant species. Richness of vagrant species is presented as the total accumulated value (Accum. Vagrant spp.) and the adjusted value takes into account that irregular vagrants do not constantly add to the species richness (Adj. Vagrant spp.).

**Figure 25.** Change of accumulated richness of dispersing species that have arrived to Galapagos in the 20th century, human population in Galapagos between 1938 and 2015 and the number of tourist per year (divided by 10) between 1979–2015
Change of accumulated richness of non-native dispersing species (top) and native dispersing species (bottom) that have arrived to Galapagos in the 20th century, human population in Galapagos between 1938 and 2015 and the number of tourist per year (divided by 10) between 1979–2015. Dispersing species are separated into resident species and vagrant species. Richness of vagrant species is presented as the total accumulated value (Accum. Vagrant spp.) and the adjusted value takes into account that irregular vagrants do not constantly add to the species richness (Adj. Vagrant spp.).

**Figure 26.** Change of accumulated richness of non-native dispersing species (top) and native dispersing species (bottom) that have arrived to Galapagos in the 20th century, human population in Galapagos between 1938 and 2015 and the number of tourist per year (divided by 10) between 1979–2015.
Growth curves are different between native and non-native dispersing species. Growth patterns for resident non-native species are basically the same as those previously noted for resident species because most species that have been able to establish self-sufficient populations are non-native. Meanwhile, few native species have established self-sufficient populations. Those that have been successful have primarily done so after a long period of time and in all cases after the mid-1950s. Vagrant non-native and native species show increasing but irregular patterns, although the accumulated richness of non-native species is growing exponentially, while that of native species is growing at a steadier pace. Interestingly, adjusted richness patterns show clear differences between non-native and native species. Richness is higher for non-native species, but most species are irregular (one out of 10); richness is lower for native species but some species are rather regular dispersers (three out of eight) (Figure 26; Table 7).

Information about the establishment, spread, dominance and impacts of dispersing amphibians, reptiles and birds in Galapagos biodiversity is still incomplete. After the discovery of the Galapagos Archipelago in 1535 and before the agricultural colonisation that started in the late 1950s, only two dispersing species were known in Galapagos (Gonatodes caudiscutatus and feral Gallus gallus), both of which have had established populations since the late XIX century. After the agricultural colonisation, 27 dispersing species (90%) arrived at the archipelago, eight of which were able to establish self-sufficient populations. Between 1990 and 2017, only one species has established self-sufficient populations. In total, ten dispersing species have been able to established populations in Galapagos, including one species of amphibian (Scinax quinquefasciatus), four species of reptiles (Gonatodes caudiscutatus, Phyllodactylus reissii, Lepidodactylus lugubris, Hemidactylus frenatus) and five species of birds (Gallus gallus, Neocrex erythrops, Crotophaga ani, Egretta thula, Bubulcus ibis) (Appendix 1). Except for Egretta thula, all dispersing species that have established self-sufficient populations in Galapagos were first recorded in human-made ecosystems, and all except for
*Neocrex erythrops* were first recorded in urban ecosystems in the dry lowlands of the islands.

*Gallus gallus* is the only species currently present in Galapagos with domestic and feral (or semi-feral) populations. Some feral chickens may have self-sufficient populations, but evidence is unclear. *Columba livia*, a non-native species that was introduced as domestic and established feral populations, was eradicated. *Scinax quinquefasciatus* is considered to be in its incipient stages of colonisation; this species has established large populations but only in a limited geographic range, although it was introduced recently (ca. 40 years). *Gonatodes caudiscutatus* is classified as constrained because it has large populations but only on a very limited geographic range, apparently unable to establish new populations in other areas despite being on the Galapagos for ca. 200 years. *Neocrex erythrops* and *Egretta thula* are classified as dispersed; they established populations unaided and are present on several islands, but their populations seem to be still small, although *N. erythrops* is probably increasing its geographic range and density. *Phylodactylus reissii* is also classified as dispersed, as it has small populations in Santa Cruz, San Cristobal and Isabela (established ca. 40 years ago). *Hemidactylus frenatus* is newly established, and self-sufficient populations are apparently small although already present on several islands. This species has a high potential not just to become more broadly established but to also spread successfully. Monitoring is urgently needed to understand the distribution, populations and impacts of *H. frenatus*. *Bubulcus ibis* is a successful native dispersing species, having been able to establish large populations across the archipelago. *Lepidodactylus lugubris* and *Crotophaga ani* are non-native species classified as successful because they have large populations established on many islands. Since *L.*

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23 Personal comments by Carlos Valle, Paul Greenfield and Ben Hasse in August 2017.
lugubris, P. reissii, H. frenatus, and C. ani have self-sufficient and spreading populations; they are classified as invasive species.

6.3.2 Analysing dispersing species and their occupied ecosystems in Galapagos

Almost all native and non-native dispersing species in Galapagos have been recorded in urban spaces in the lowlands. In fact, all irregular vagrants have been reported and usually intercepted in urban ecosystems in the lowlands, with the exception of Lampropeltis micropholis. In addition, the resident native Neocrex erythrops has usually been recorded in the highlands, in urban and agricultural ecosystems, although it may inhabit natural ecosystems as well. The following species have not been recorded in agricultural spaces: Rhinella horribilis, Pristimantis unistrigatus, Lepidodactylus lugubris, Hemidactylus frenatus, Iguana iguana and Boa constrictor.

While there are no native amphibians in Galapagos, Scinax quinquefasciatus, the only amphibian established in Galapagos, has self-sufficient populations in suburban areas in the lowlands of Isabela, small populations in urban spaces in the lowlands of Santa Cruz and probably newly established populations in San Cristobal. There are no records of any species of amphibians in the natural environment of the Galapagos National Park.

Gonatodes caudiscutatus has populations that apparently fluctuate between uncommon and constrained in urban spaces in the lowlands of San Cristobal Island, where it is restricted to moist anthropic environments, including gardens, parks and other urban green spaces. On Baltra and Santa Cruz islands, little is known about the species’ distribution. It is probable that a small population is already established on Santa Cruz Island, although it likely remains non-common. Interestingly, G. caudiscutatus is the first reptile to establish non-native populations on the islands in historic times. Habitats where G. caudiscutatus occur on mainland Ecuador are very similar to those which it inhabits on the Galapagos Islands. Phyllodactylus reissii has dispersed

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populations in urban areas in the lowlands of Santa Cruz Island and apparently newly established and expanding populations in urban areas in the lowlands of San Cristobal and Isabela islands. Amongst reptiles, only *Gonatodes caudiscutatus* and *Phyllodactylus reissii* have been found to be marginally present in natural areas, usually in ecotones between suburban/agricultural areas and natural ecosystems. *Lepidodactylus lugubris* has successful populations in urban and suburban areas in the lowlands of Santa Cruz, San Cristobal and Isabela islands, always in moist environments in coastal areas (i.e., artificially watered urban areas and mangroves). It has also established populations in the town of El Progreso, located in the highlands of San Cristobal, where it remains restricted to human buildings. However, at least the populations of *L. lugubris* on San Cristobal have decreased in recent years, apparently due to competition with the Common House Gecko *Hemidactylus frenatus*. *H. frenatus* was first reported in urban areas of Isabela Island and currently seems to be have established incipient populations on Isabela and San Cristobal islands. Only one species of reptile, *Iguana iguana*, is a regular vagrant. It has been recorded in the urban areas of Santa Cruz, San Cristobal and Isabela islands. All reports of *I. iguana* apparently correspond to isolated individuals that were not able to establish populations and were ultimately intercepted.

*Gallus gallus* was introduced as a domesticated fowl in urban and agricultural areas of Galapagos and some populations became feral and are apparently present on all inhabited islands of Galapagos. However, it remains unclear if those populations are indeed self-sufficient and truly feral (i.e., completely independent of human care). *Columba livia* also started as domestic in urban areas, but feral populations eventually dispersed into urban, peri-urban and agricultural areas. *Crotophaga ani* is not uncommon in urban and suburban areas in all four inhabited islands, but its most dense populations are found in agricultural lands. *Crotophaga ani* has been recorded in natural ecosystems, although in lower abundances and densities than in agricultural areas.
Nine species of terrestrial birds recorded on the Galapagos have reached the islands most probably by natural dispersion from mainland South America in recent (historic) times\(^ {24} \): *Podilymbus podiceps, Egretta thula, Egretta caerulea, Bubulcus ibis, Dendrocgygna autumnalis, Nomonyx dominicus, Neocrex erythrops, Porphyrio martinicus, Progne tapera, Zenaida auriculata, Coccyzus lansbergi* and *Coereba flaveola*. Except for the last two species whose geographical occurrence remains largely unstudied, all other species have been found in urban or agricultural ecosystems. Only *Egretta thula* and *Bubulcus ibis* have extended across large parts of the archipelago, into both human-modified and natural ecosystems. While there are few records of most of these species in the archipelago, the following species have become regular visitors or have established self-sufficient populations: *Egretta thula, Neocrex erythrops, Porphyrio martinicus* and *B. ibis*. All of these species are herein considered native species of Galapagos. Although humans did not mediate their arrival processes, all of them have been able to take advantage of and establish populations in human-modified ecosystems.

### 6.3.3 Reviewing impacts by dispersing species in Galapagos

*Rhinella horribilis* and *Pristimantis unistrigatus* have not established populations in Galapagos, and thus have not influenced the local biodiversity. No information is available about potential or evidenced impacts by any non-native *R. horribilis\(^ {25} \).* Comparatively, the Eastern Cane Toad *Rhinella marina* has been successfully introduced to many areas around the world (Easteal 1981; Lever 2003) and is one of the most studied introduced species, especially in Australia. The main demonstrated ecological impact of *R. marina* is the decline

\(^ {24} \) Other bird species recorded as vagrants at Galapagos can be classified as oceanic wanderers or as stray boreal migrants (Wiedenfeld 2006; Jiménez-Uzcátegui et al. 2015).

\(^ {25} \) Only two population of *Rhinella horribilis* have been reported to be established completely outside of their native range: in Florida (King & Krakauer 1966; Easteal 1981) and in the valleys of the Hoya de Guayllabamba in the northern Andes of Ecuador (pers. obs.). However, no studies about impacts by those populations on native biodiversity have been published.
of native Australian predators, caused by its toxicity when ingested (Shine 2010). Also, there are no documented introduced populations of any species of the genus *Pristimantis* (Lever 2003, Kraus 2009), thus no known related impacts.

*Scinax quinquefasciatus* is insectivorous, thus its predation on native invertebrate fauna has been identified as a potential impact on Galapagos biodiversity (Phillips et al. 2012). However, there are no systematic studies regarding its diet or evidence about any real impact. General observations about its diet reveal that the species is a generalist predator that consumes native and non-native invertebrates. It is unknown how the increasing numbers of frogs on Santa Cruz and Isabela may alter local trophic cycles, especially with regards to their large biomass consumption. In addition, due to increased populations sizes, noise nuisance as a public concern has been raised. Local residents of agricultural areas of Santa Cruz have begun to report that the frogs’ calls disturb their normal evening activities.

Impacts by *Gonatodes caudiscutatus* on Galapagos biodiversity are unknown but have been suspected to be little or even non-existent (Hoogmoed 1989; Olmedo and Cayot 1994; Phillips et al. 2012). Competition or exclusion of endemic geckos is unlikely, due to body size, habitat and microhabitat differences (*G. caudiscutatus* being diurnal, and all the other geckos nocturnal). Although *G. caudiscutatus* is insectivorous, it probably eats mainly non-native and widespread invertebrates which predominate in urban and agricultural environments, although there are no studies confirming its diet. Recent data have revealed that *G. caudiscutatus* are important prey of *Pseudalsophis* snakes (D. F. Cisneros-Heredia, unpubl. data).

*Phylodactylus reissii* is native to dry forests and scrubland as well as to rural, suburban and urban areas in central western Ecuador to north-western Peru (Dixon & Huey 1970). In Galapagos, *P. reisi* remains mostly restricted to urban, suburban and rural areas. In areas of Puerto Ayora where *P. reissi* is
dominant, it appears to have displaced the endemic *P. galapagensis*; they rarely cohabitate the same environments (Hoogmoed 1989; Olmedo & Cayot 1994). No information about possible exclusion mechanisms or interactions has been published. If *P. reissii* were to expand to natural areas, it could impact endemic *Phyllodactylus* (Hoogmoed 1989; Olmedo & Cayot 1994; Phillips et al. 2012).

The consequences of the introduction of *Lepidodactylus lugubris* to Neotropical areas, including Galapagos, are unclear (Hoogmoed and Avila-Pires 2015). No impacts on Galapagos biodiversity have been reported (Olmedo and Cayot 1994; Phillips et al. 2012). Competitive interactions between *L. lugubris* and geckos endemic to the Galapagos have apparently not affected endemic species (M. Altamirano 2002 cited in Phillips et al. 2012). Although *L. lugubris* is insectivorous, it probably eats mainly non-native and widespread invertebrates. To date, there are no known studies about its diet.

Due to the recent arrival of *Hemidactylus frenatus*, no information is available about any type of interactions or effects of this species on the endemic *Phyllodactylus* geckos. However, its arrival has raised concerns due to reported impacts on native fauna in other areas where it is established (Torres-Carvajal & Tapia 2011; Torres-Carvajal 2015). *Hemidactylus frenatus* has outcompeted and excluded non-native *Lepidodactylus lugubris* from several Pacific islands through competitive exclusion (Petren & Case 1998; Kraus 2009). Preliminary evidence suggests that *H. frenatus* may also be excluding *L. lugubris* in San Cristobal. In 2009, *L. lugubris* was the most common gecko in urban environments of that town. However, in 2017, only once this species was recorded and all other records corresponded to *H. frenatus*. On the Mascarene Islands, *H. frenatus* contributed to the decline and population extirpation of

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26 At least one study about interactions between non-native and endemic geckos in Galapagos has been conducted but remains unpublished (M. Altamirano’s PhD dissertation, cited by Phillips et al. 2012).
endemic geckos of the genus *Nactus* (Cole et al. 2005). Furthermore, it could carry novel parasites that may impact native reptile species (Hoskin 2011). However, no information is available about interactions between Galapagos-endemic *Phyllodactylus* and *H. frenatus*.

*Lampropeltis micropholis* is a terrestrial snake which is active during the day and night and which eats a large variety of vertebrates and invertebrates (Williams 1988). There are no records of non-native populations of *L. micropholis* established outside of its range or studies of insular populations. For comparison, a study of the diet of insular populations of *Lampropeltis polizona* on Isabel Island, Mexico showed that they fed on different species of terrestrial lizards and nestlings of ground-nesting marine birds, including the Blue-Footed Booby *Sula nebouxii*. It was also found that they avoided arboreal geckos and tree-nesting birds. The California Kingsnake *Lampropeltis californiae* became established on Gran Canaria Island, where its main evidenced ecological impact is predation on endemic lizards (Pether and Mateo 2007; Cabrera-Pérez et al. 2012).

No established populations of *Iguana iguana* occur in Galapagos. In some islands of the Caribbean where it has been introduced, *I. iguana* has displaced the native *I. delicatissima* by hybridisation (Powell & Henderson 2005, Lever 2003; Kraus 2009; Powell et al. 2011; Vuillaume et al. 2015). Since inter-generic hybridisation has been reported in iguanas (Rassmann et al. 1997; Jančúchová-Lásková et al. 2015), the establishment of *I. iguana* in Galapagos could pose a threat for the endemic iguanas of the genus *Amblyrhynchus* and *Conolophus*.

The main potential impact of the domestic chicken on native fauna is the spreading of infectious diseases to native birds (Wikelski et al. 2004; Gottdenker et al. 2005; Hernandez-Divers et al. 2008; Soos et al. 2008; GISD 2010; Deem et al. 2012). Yet, this threat has not been demonstrated and the evidence for it remains theoretical and correlative (GISD 2010; Baker et al. 2014). The Global Invasive Species Database (GISD 2010) mentions that *G.*
*gallus* could negatively impact native vertebrates, but their only reference (Varnham, 2006) is anecdotal and based on a different species (Green Junglefowl *Gallus varius*). Phillips et al. (2012) noted: “no impacts [by *G. gallus*] to the [Galapagos] native biota have been documented”. I present the first evidence of predation on squamate reptiles by domestic chickens in Galapagos. On June 2009, I observed a hen attacking a small Galapagos Racer *Pseudalsophis biserialis* in a private yard next to the road between Puerto Baquerizo Moreno and El Progreso, San Cristobal Island. The hen pecked on the snake’s head and body, after which it seized the snake with its beak and started to run, chased by another hen. Eventually, the hens carried the snake into a shed where they took cover. On July 2009, I observed a hen chasing a small Dwarf Gecko *Gonatodes caudiscutatus*, apparently found while foraging among some leaf litter and rocks in a private yard in El Progreso, San Cristobal Island. The gecko managed to flee and hide under rocks. On July 1997, I observed a rooster pecking and eating a dead Peters’ Leaf-toed Gecko *Phylodactylus reissi* in a vacant urban lot at Santa Cruz Island. *Gallus gallus* mainly eats seeds and other plant material, although it is an omnivorous bird. Red Junglefowl, the wild ancestor of the Domestic Chicken, occasionally eats lizards and snakes (Ali & Ripley 1980). Reports of attacks and predation on squamate reptiles by Domestic Chickens are rare but have been reported worldwide (Guthrie 1932, Bell 1996; Powell and Henderson 2008; Mesquita et al. 2009; Sasa et al. 2009; pers. obs.). Scarcity of records seems to suggest that chicken predation on lizards and snakes is an opportunistic, yet atypical behaviour. However, it could also be due to under-reporting and paucity of herpetologists surveying chicken yards. Free-range chickens can move over hundreds of metres away from their shelters to forage, usually towards hedges and borders where encounters with small snakes and lizards would be more prone to occur, though such encounters would remain largely unwitnessed.

The main potential impact of the Domestic Pigeon on Galapagos fauna was the spreading of the protozoan parasite *Trichomonas gallinae* to the endemic
Galapagos Dove *Zenaida galapagoensis* (Harmon et al. 1987; Phillips et al. 2003). Indirect evidence for this threat was anecdotal and correlative, based on the presence of the parasite *Z. galapagoensis* on islands were pigeons occurred (and their absence in pigeon-free islands) and on the decline of *Z. galapagoensis* on islands populated by pigeons (Baker et al. 2014; Wikelski et al. 2004).

*Crotophaga ani* is mainly insectivorous, but also consumes plant material (especially fruits) and vertebrates (including lizards, snakes, frogs, birds and mice) (Bent 1940; Skutch 1959; Olivares & Munves 1973; Rosenberg et al. 1990; Burger & Gochfeld 2001; Payne & Sorensen 2005; Repenning et al. 2009; Connett et al. 2013). Predation on animals seems to increase during the *C. ani*’s breeding period, which coincides with the wet season when *C. ani* apparently prefers grasshoppers and other orthopterans (Davis 1940; Payne & Sorensen 2005; Repenning et al. 2009). Hymenopteran insects, such as euglossine bees and social wasps *Polystes* spp., have been reported as part of the diet of *Crotophaga ani* (Skutch 1959; Rosenberg et al. 1990; Raw 1997; Burger & Gochfeld 2001; Repenning et al. 2009). Two studies about the diet of *C. ani* on Santa Cruz Island showed that they consume hymenopterans. Rosenberg et al. (1990) reported hymenopterans in only four of 24 dissected gizzards. Connett et al. (2013) found twelve *X. darwini* in the gizzards of 12 *C. ani*, but, in this case, it was the most frequently consumed invertebrate species.

Four potential impacts by *Crotophaga ani* on Galapagos biodiversity have been postulated (Rosenberg et al. 1990; Grant & Grant 1997, Dvorak et al. 2004; Fessl et al. 2010):

(i) Propagation of invasive plants. Available evidence suggests that *Crotophaga ani* has a high potential to propagate introduced plants, including the invasive Raspberry *Rubus niveus* and Wild Sage *Lantana camara* (Guerrero & Tye 2011).
(ii) Predation on native fauna. Rosenberg et al. (1990), Guerrero & Tye (2011) and Connett et al. (2013) reported predation of Galapagos native invertebrates, lizards and Darwin Finch nestlings by *Crotophaga ani*.

(iii) Competition with native avifauna, which remains untested and speculative.

(iv) Introduction of avian diseases, also untested and speculative.

Nonetheless, Phillips et al. (2012; *contra* Rosenberg et al. 1990) stated that the Smooth-billed Ani is “a low priority alien species, not having been attributed with any serious impacts to native species, although it is likely that they have some effects on native [fauna]”.

Herein I present information that constitutes the first evidence of a probable major impact on an endemic invertebrate due to predation by *Crotophaga ani*. Between 08–16 June 2009, I observed six groups of *C. ani* assiduously predating on the Galapagos Carpenter Bee *Xylophaga darwini* at six different locations on San Cristobal Island. Carpenter bees in high densities were foraging on blooming trees in the Dry Zone, usually near the coast. I observed one group of *C. ani* over a 30-minute period and the other five groups during 15-minute periods each. In total, the six groups consumed 661 bees over the observation periods. Each bird captured an average of 8.5±4.4 (range = 4–15) bees per 15 minutes. *Crotophaga ani* continued preying upon bees after each observation period ended. Despite the continuous attacks, the bees did not disperse and more individuals continued to arrive, as they were attracted by the flowers. Although large numbers of the non-native Social Wasp *Polistes versicolor* were also present, as well as some butterflies, *C. ani* largely ignored them.

6.3.4 Describing arrival pathways of dispersing species

Eight (32%) non-native amphibians, reptiles and birds in Galapagos arrived as domestic animals, five (20%) as pets and one (4%) as (unsuccessful) biocontrol (Appendix 1). All domestic animals, pets and biocontrols were
brought to the islands deliberately. However, most (44%) non-native amphibians, reptiles and birds were unintentionally translocated to the Galapagos as hitchhikers aboard airplanes or boats (Appendix 1). While data for most species is incomplete, this hypothesis is supported by VCCDRS specimens of *Scinax quinquefasciatus* collected in several locations, including on a boat on Santa Cruz and at the airport of San Cristobal. *Sicalis flaveola* was found inside of an airplane (CDF 2016).

Six hitchhiking species arrived on Galapagos before the quarantine inspection system started in June 2000, and nine species were first recorded after. Among these previous hitchhikers, *Rhinella horribilis*, a large toad (> 70 mm in old juveniles, >100 mm in adults), would now be unlikely to bypass quarantine inspections. The only known record of *R. horribilis* in Galapagos was made five years before the quarantine system started. *Lampropeltis micropholis* and *Iguana iguana* are large reptiles (> 600 mm) and both reached Galapagos after 2000 (it is uncertain how they bypassed quarantine). In contrast, *Scinax quinquefasciatus*, *Pristimantis unistrigatus*, *Gonatodes caudiscutatus*, *Phyllodactylus reissii*, *Lepidodactylus lugubris* and *Hemidactylus frenatus* are relatively small and with rather cryptic colorations (brownish). They could thus be easily overlooked during quarantine inspections, and multiple translocations could still occur. Gill et al. (2001) reported live interception cases of *S. quinquefasciatus*, *L. lugubris* and *H. frenatus* in Ecuadorian banana shipments arriving to New Zealand, thereby demonstrating its ability to be translocated and to survive physiological stress during long trips.

Most hitchhiking species that reach Galapagos do so via air and maritime ports, or the surroundings of cargo warehouses. However, not all translocations come directly from ports of shipment. *Lepidodactylus lugubris* does not occur in areas with air or maritime ports in mainland Ecuador with connections to the Galapagos, including Manta, Guayaquil and Quito. *Lepidodactylus lugubris* was first recorded in mainland Ecuador in Esmeraldas in 1963 (Fugler 1966). Currently, it inhabits the humid lowlands and foothills
along north-western Ecuador, restricted to urban and suburban areas in the provinces of Esmeraldas and Santo Domingo de los Tsáchilas (Fugler 1966; Schauenberg 1968; Hoogmoed & Avila-Pires 2015). It is absent from arid central and south-western lowlands of Ecuador. The translocation of *L. lugubris* to Galapagos was possibly facilitated by horticultural cargo arriving from Esmeraldas or from other countries where the species was already present, such as Colombia or Panama.

Human-facilitated transportation has provided opportunities for amphibians, reptiles and birds to reach Galapagos, independent of their physiological adaptations to salinity or to long trips. However, upon arrival, they still need to withstand the arid environments of the Littoral and Dry zones, where freshwater is almost completely absent under natural conditions on most islands. While all non-native frogs, reptiles and birds reported in Galapagos are able to survive in arid environments to some degree, at least frogs and small geckos are still dependent on some humidity. Local and regional climate changes can have an important effect on the establishment and distribution of non-native species in Galapagos (Snell and Rea 1999). Higher rainfall during El Niño events (e.g. 1997–1998 and 2009–2010) was a major factor in the establishment of *Scinax quinquefasciatus* populations on Isabela and in the expansion of *Crotophaga ani* (Snell and Rea 1999; Pazmiño 2011). El Niño in 1997–1998 increased environmental humidity and diluted salinity in the lagoons of Puerto Villamil, allowing *S. quinquefasciatus* to thrive. After the El Niño event of 2009-2010, *S. quinquefasciatus* was able to reach the humid agricultural areas of Bellavista (Pazmiño 2011).

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27 The first specimen of *Lepidodactylus lugubris* from America was collected in Panama in 1916 (Fugler 1966; Hoogmoed & Avila-Pires 2015). G.K. Noble collected it during his trip for the Harvard Peruvian Expedition (Collection catalogue, Herpetology, Museum of Comparative Zoology, Harvard University). The gecko was collected just two years after the opening of the Panama Canal. It was probably translocated on boats coming from Hawaii or Oceania (Smith & Grant 1961). By 1941, *L. lugubris* had already reached Colombia (Daza et al. 2012; Hoogmoed & Avila-Pires 2015).
Artificially watered green urban and suburban areas such as parks and gardens have played an important role in the establishment of non-native amphibians and reptiles in Galapagos. They can act as refuges for newly established species, provide resources to large local populations and facilitate intra and inter-island dispersion across inhabited areas (Ineich 2010). All non-native geckos are mainly found in green urban and suburban areas. Genetic evidence from Isabela Island populations of *Scinax quinquefasciatus* (Pazmiño 2011) and recurring records of *S. quinquefasciatus* from Santa Cruz Island and *G. caudiscutatus* at San Cristóbal suggest that there were multiple introduction events for both species. Before El Niño’s impact, these populations were apparently able to survive thanks to artificially watered green urban and suburban areas.

Most hitchhiking amphibian and reptiles are usually translocated by freight or accidentally arrive on airplanes or boats after having lived in the crevices/compartments of these vehicles. However, they can also be transported inside tourist luggage. On August 2009, a live *L. lugubris* was unintentionally translocated in my handbag from San Cristóbal Island to Guayaquil. It probably entered my bag at a restaurant near the dock, since I never saw *L. lugubris* at the USFQ Galapagos Campus where I stayed. I noticed its presence after opening my bag in Guayaquil. Furthermore, this shows that non-native species translocations may work in both ways, exchanging individuals between populations of Galapagos and the continent.

Large hitchhiking reptiles and birds can accidentally enter closed areas inside freight airplanes and boats, although they are easily detected and intercepted (like the individual *Sicalis flaveola* in Galapagos). However, probably the most

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28 In comparison with Santa Cruz Island, the area of urban and suburban gardens in San Cristóbal is smaller. This limited habitat availability is apparently the reason why *Gonatodes caudiscutatus* has small and restricted populations in the lowlands of San Cristóbal and why *Scinax quinquefasciatus* has not become established on that island (despite its first record there in 2000).
common hitchhiking situation takes place when large reptiles and birds stay on decks and other exterior structures of passenger and cargo boats. They can hitchhike after boats have gone through the departure port inspections, survive for several days, remain overlooked and swim or fly towards land before the boat reaches controls in the arrival ports. *Iguana iguana* and *Quiscalus mexicanus* have likely arrived in this way to the Galapagos. Several hitchhiker bird species are known to have arrived and established themselves on islands around the world: the House Sparrow *Passer domesticus* on the Canary and Maldives islands, the Spanish Sparrow *Passer hispaniolensis* on the Canary Islands, the Pale-billed Mina *Acridotheres cinereus* on Borneo Island, the Red-Vented Bulbul *P pictus cafer* on the Marshall and Hawaii islands, the House Crow *Corvus elegans* on the Socotra Islands and Australia, and the Great-tailed Grackle *Quiscalus mexicanus* on Jamaica (Haynes-Sutton et al. 2010; Lever 2010; Suleiman & Taleb 2010).

6.3.5 Identifying islands where dispersing species may establish themselves

If further amphibian, reptile and bird introductions are to be stopped in Galapagos, it is important to establish which islands are vulnerable to those introductions and to understand the general profiles of potential hitchhikers.

The four populated islands are the most vulnerable to the translocation of non-native species because they have air and maritime ports as well as a large flux of local people and tourists. Isabela Island is apparently the most vulnerable island to the establishment of amphibians because it has freshwater wetlands next to the city and harbour\(^\text{29}\). Santa Cruz, San Cristobal and Floreana islands have coastal lagoons with significantly more salinity than Las Diablas lagoon in Isabela (Gelin & Gravez 2002), thus it is unlikely that amphibians would be able to easily establish themselves there. The moist highland zones of all

\(^{29}\)The largest coastal lagoon of Isabela, Las Diablas, is next to the town of Puerto Villamil. Its low salinity levels (6–10 gL\(^{-1}\), Gelin & Gravez 2002) allow the reproduction of *S. quinquefasciatus*. 
populated islands are especially vulnerable to the introduction of non-native amphibians, reptiles and birds, due to the presence of mesic environments with extensive agro-urban areas and wetlands. Furthermore, the moist zones in the highlands of Isabela are closer to the coast, making it easy for non-native species to reach a mesic environment where they could survive and establish themselves.

6.3.6 Identifying species as potential hitchhikers

Intentionally introduced species, such as pets and domestic animals, are rather easy to detect and identify because they are usually conspicuous and recognisable. However, hitchhiking species create the real predicament for official quarantine. Hitchhiking species are usually inconspicuous, difficult to identify and hard to find. A key factor in the control of hitchhiking species is the proper training of port personnel and airplane and boat crews such that they may correctly identify, restrain and handle non-native hitchhiking animals in airplanes, boats and ports. Although the species lists herein provided could be improved, I hope they will provide valuable information for the Agency for Regulation and Control of Biosecurity and Quarantine for Galapagos (ABG) and other organisations involved in the conservation and management of the archipelago (including the Consejo de Gobierno del Régimen Especial de Galapagos CGREG, Ministerio de Agricultura, Ganadería, Acuacultura y Pesca MAPAG, Parque Nacional Galápagos PNG and the Ministerio del Ambiente MAE).

A cautionary note: Some reptiles and birds from mainland Ecuador may look similar to those native to Galapagos. For example, the Galapagos endemic geckos of the genus *Phyllodactylus* could be confused with the non-native *Phyllodactylus reissii*; and the native *Setophaga petechia* has been confused in the past with the non-native *Sicalis flaveola*. Guides and manuals specifically tailored to crew and other control personnel should be created to avoid confusion and to facilitate the reinforcement of control measures.
Amphibian and reptile species with higher hitchhiking potential to Galapagos seem to be characterised by: (i) inconspicuous colouration and small to medium body size; (ii) adaptations to arid environments and/or anthropogenic areas; (iii) frequent occurrence in the surroundings of cargo warehouses or in agricultural areas; and (iv) living in the Pacific lowlands of central Ecuador, where habitats have environmental conditions similar to those found in the Galapagos and in the main ports in which freight airplanes and boats that travel to Galapagos are located.

In mainland Ecuador, there are six frog species matching this hitchhiker profile: *Scinax quinquefasciatus*, *Pristimantis achatinus*, *Barycholos pulcher*, *Engystomops pustulatus*, *Trachycephalus jordani*, *T. typhonius*, and *Rhinella horribilis*. While the first species is already established in Galapagos, the remaining five have a high probability of settling in Galapagos if they are allowed to reach the island. Furthermore, these species have additional advantages favouring their establishment in insular environments: *Pristimantis achatinus* and *B. pulcher* are terrestrial breeders with direct development; *E. pustulatus*, *S. quinquefasciatus* and *R. horribilis* are opportunistic breeders that can reproduce even in small puddles; and *E.

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30 Which contributes to their hard detection and improves their survivorship (Olson et al. 2012)

31 Adaptation to desiccation conditions has also enhanced tolerance to salinity in some amphibians (Balinsky 1981; Wells 2007), thus making it easy for them to survive in low-salinity lagoons like Las Diablas in Isabela Island. The three species of *Scinax* that have become established on islands as cargo hitchhikers are adapted to arid environments or anthropogenic areas on their native distributions: *Scinax quinquefasciatus*, *S. x-signatus* and *S. ruber* (Breuil and Ibéné 2008; Breuil 2009; Kraus, 2009; Powell et al. 2011). The first two are also known to be adapted to breed in marshes with low salinity (Jiménez-Uzcátegui et al. 2007; Ríos-López 2008; pers. obs.). It seems that *Scinax* species that are able to adapt to open habitats show some tolerance to salinity.

32 Frogs that are common in these have easy access to freight or have a great chance of being packed with horticultural products (Kraus et al. 1999).

33 Species that establish successful self-sufficient populations usually come from areas that have a similar climate to the jurisdiction to which they are introduced (Bomford et al. 2009).
*pustulatus, T. jordani* and *T. typhonius* can inhabit extremely arid environments with low seasonal rainfall, similar to the lowlands of Galapagos. Live *T. jordani* have been intercepted as far away as the United States of America and New Zealand in banana shipments arriving from mainland Ecuador (Hartweg 1955; Gill et al. 2001). Although large adult *R. horribilis* should be intercepted during quarantine, juveniles are small and inconspicuous. However, desiccation is a major mortality factor for juveniles (Zug & Zug 1979). But, if they were able to find shelter and wet conditions, they could survive travelling to Galapagos. There are eleven species of squamate reptiles matching the hitchhiker profile in mainland Ecuador: *Gonatodes caudiscutatus, Hemidactylus frenatus, Phylodactylus reissii, Iguana iguana, Lampropeltis micropholis, Boa constrictor, Dipsas elegans, Erythrolamprus epinephelus, Mastigodryas sp. (cf. boddaerti), Mastigodryas pulchriceps, and Oxybelis aeneus*. The first five species have already been recorded in Galapagos.

Although little information is available on hitchhiker birds, at least the following features seem to characterise potential hitchhiker birds to the Galapagos: (i) being adapted to arid environments or anthropogenic areas which would allow them to survive in the lowlands of Galapagos; (ii) occurring frequently in the surroundings of main ports of freight airplanes and boats to Galapagos, with higher probability to enter closed areas inside freight airplanes and boats or wander around boat decks; (iii) habit to fly at least short distances over the sea, so it can reach departed boats; and (iv) the adaptability to build nests within human-made structures, which attract reproductive adults into boats. Since birds are active and noticeable animals, their detection and capture should be fairly easy during quarantine procedures.

To guide such training, I provide a shortlist of birds from mainland Ecuador that match the potential hitchhiker profile: Eared Dove *Zenaida auriculata, Thaupis episcopus*, Saffron Finch *Sicalis flaveola*, Rufous-collared Sparrow *Zonotrichia capensis*, Shiny Cowbird *Molothrus bonariensis*, Great-Tailed
Grackle *Quiscalus mexicanus* and the House Sparrow *Passer domesticus*. Of these birds, two have been already been recorded on Galapagos and are discussed above. There are records of *Z. auriculata* on Champion Islet, Santa Cruz and Baltra islands (Wiedenfeld 2006; Loranger 2012). Although all these areas are in or close inhabited islands (and to the airport in Baltra), their origin cannot be directly attributed to hitchhiking since this species is capable of oceanic dispersing (Baptista et al. 2013). Of all the birds herein listed, *M. bonariensis* could be a major threaten if it were to establish itself on the Galapagos. This brood parasite could seriously affect endemic and otherbird species with small populations on the islands (Oppel et al. 2004). Its populations have expanded to the surroundings of the two air and maritime ports of Guayaquil and Quito (Cisneros-Heredia et al. 2015; Crespo-Pérez et al. 2016; pers. obs.).

6.4 Discussion

Data presented in this study strongly evidence temporal and spatial patterns that support the hypothesis that habitat change has facilitated natural colonisations and invasions by amphibians, reptiles and birds dispersing species in Galapagos.

Between the time of the discovery of the Galapagos in the XVI century and the mid 1950s, vagrant dispersing species were not present in the archipelago and species richness of resident dispersing species was very low. This coincides with the historical period during which Galapagos was sparsely populated and habitat change was limited to small urban and surrounding agricultural areas (Snell et al. 2002; Walsh et al. 2010). In fact, the only two resident dispersing species were *Gallus gallus*, as feral populations in the surrounding agricultural areas, and *Gonatodes caudiscutatus*, which was probably transported by the first settlers as a hitchhiker and was able to easily adapt to Galapagos because its native ecological niche is extremely similar to that which it assumed in the archipelago.
In 1956, the Instituto Ecuatoriano de Reforma Agraria y Colonización (IERAC) initiated a plan of agricultural colonisation developed under the national policies to transform “abandoned” lands (i.e., natural environments) into “productive” areas (i.e., agricultural ecosystems) (Grenier 2007). This plan promoted the first influx of migrants from mainland Ecuador that arrived to Galapagos and started to work there as farmers. By 1962, almost 60% of the economically-active population of Galapagos was working in agricultural activities (Grenier 2007). The most affected areas were the moist highland areas, due to the availability of freshwater and rich volcanic soils. Habitat change was significant, with between 70 and 95% of the highlands of the populated islands were transformed into agricultural lands (Snell et al. 2002; González et al. 2008). A significant and fast increment of all dispersing species started after the agricultural colonisation period. In particular, this period was particularly important to the arrival and establishment of self-sufficient populations of several native and non-native both native and non-native species. The islands most affected by habitat changes were San Cristobal and Santa Cruz, and both are the islands with the highest number of dispersing species.

In 1959, the Galapagos National Park was established by the government of Ecuador in order to protect all areas that were not colonised. About 97% of Galapagos was included in the national park (González et al. 2007). However, processes were slowly developed and policy was not immediately or stringently reinforced when the park began operations in 1968; rather, and governmental and private conservation institutionalisation in Galapagos really started after the 1970s and flourished between 1980-1990s (Snell et al. 2002; González et al. 2007, Grenier 2007, Walsh et al. 2010).

While the declaration of the national park stopped habitat changes in additional areas of Galapagos, the real key factor that changed the panorama of Galapagos was tourism, which started in the early 1970s and continues to be the main economic activity in the archipelago. Tourism transformed
Galapagos into a very attractive place to work and thousands of new residents arrived from mainland Ecuador to work in such lucrative businesses (Kerr et al. 2004; Epler 2007). These new socioeconomic interactions produced a new set of habitat changes, including the expansion of urban environments in the lowlands (Walsh et al. 2010). Incremental resident and tourist populations demanded new types of towns with green spaces and infrastructure, which provided excellent moist habitats for arriving species that otherwise would not have been able to survive in the dry natural ecosystems of the lowlands. All three species of amphibians in Galapagos perfectly exemplify the importance of green urban spaces for the establishment of animals that require moist or even freshwater environments.

Increasing populations also generated a growing demand of products including food, bottled water, fuel and building materials, which in turn transformed the web of transportation between mainland Ecuador and Galapagos, thus breaking the historical biogeographic barrier that isolated the islands from each other and from the continent (González et al. 2008). Dispersing species richness grew increasingly until the 1980s-1990s. In particular, vagrant species started to accumulate at a growing rate parallel to that of the expanding human populations.

The establishment of more rigorous policies to control introduced species have apparently helped to relatively stabilise the accumulative curve of dispersing species after the 1990s. In particular, the establishment of quarantine processes in 1999 was one of the key strategies to intercept vagrant species and to diminish the rate of establishment of resident species (Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012). Interestingly, after 2010, an increase in vagrant and resident species was again detected. This apparently coincided with new established policies for the management of freight arriving on ships from the continent. Until the early 2010s, freight arrived from mainland Ecuador in medium-sized ships and cargo was first loaded onto barges and then transported to the ports on the different islands. The intermediary
process of barges allowed for a higher level of control and quarantine. However, over the last five years, large-sized ships put their cargo directly into containers that are loaded into the island ports, allowing for a myriad of hitchhiker to go unnoticed. This was how two 1-meter-long snakes and several iguanas arrived in Santa Cruz.

Interestingly, when native and non-native species are compared, it is evident that their dispersion and establishment patterns are different in Galapagos. Native species are more common and regular vagrants, but their success rate to establish self-sufficient populations is low. Contrastingly, non-native species show higher levels of success in the establishment of self-sufficient populations.

Chickens have become the dominant domestic bird in all inhabited islands of the Galapagos. Several studies have discussed the possible transmission of diseases from chickens to native Galapagos fauna, its potential impacts and potential control measures (Wikelski et al. 2004; Gottdenker et al. 2005; Soos et al. 2008; Deem et al. 2012). Free-range (and feral) chickens seem to have some degree of predatory impacts on Galapagos fauna, as evidenced in this chapter. However, chicken predation on endemic fauna is probably uncommon because endemic snakes and lizards prefer dry lowland areas and most free-range and feral chickens occur in moist highland areas (CGREG 2014). On the other hand, it is possible that chickens have significant impacts on the populations of the introduced gecko *Gonatodes caudiscutatus*, the only squamate reptile of Galapagos that mainly occurs in moist highland areas (i.e. agricultural lands at San Cristobal Island). Nevertheless, chicken predation probabilities increase in urban and suburban areas where endemic snakes and endemic and non-native lizards and chickens co-occur.

Soos et al. (2008) suggested several regulatory and management procedures focused on preventing the spread of poultry diseases to wild birds, including the elimination or reduction of free-range chickens. Eliminating free-range
farming may be impractical due to cultural, social and economic factors. A more plausible option would be to promote free-range poultry farming with biosecurity measures that reduce the interaction between chickens and wildlife. Some measures should include: building well-kept fences to prevent chickens from leaving the farm and to stop them from foraging on hedges and other vegetated areas; creating a peripheral ring without vegetation made of rocks or wreckage around the fences, coops and troughs and clean fenced-in pastures for poultry roaming to prevent attracting wildlife inside chicken yards. These and other measures must be established and reinforced with the active participation of Galapagos poultry owners and local and national authorities dealing with agricultural practices and wildlife conservation (including: ABG, Consejo de Gobierno del Régimen Especial de Galapagos CGREG, Ministerio de Agricultura, Ganadería, Acuacultura y Pesca MAPAG, Parque Nacional Galápagos PNG and the Ministerio del Ambiente MAE).

Of all non-native species, *Crotophaga ani* is the only species with established, self-sufficient and expanding populations into anthropic and natural areas in Galapagos. Data presented herein show that the Smooth-Billed Ani *Crotophaga ani* can heavily predate on the Galapagos Carpenter Bee *Xylocopa darwini*. Large body size and slow flight of Carpenter Bees, probably making them easier and more nutritious prey for *C. ani*, as compared with other similar species of invertebrates. Observations of six different groups of *C. ani* with an intensive predatory behaviour on *Xylocopa darwini* on San Cristobal Island suggest that is not a unique habit. Furthermore, this behaviour may be widespread since *X. darwini* is known to be part of the diet of *C. ani* on Santa Cruz Island (Rosenberg et al. 1990; Connett et al. 2013). If similar patterns of predation are consistent (at least throughout the breeding period), *C. ani* may have a severe impact on local carpenter bee populations. *Xylocopa darwini* is the only endemic bee from the archipelago (Gonzales et al. 2010, Rasmussen et al. 2012). It is a keystone pollinator species on the islands. They are the most important flower visitors and are responsible for the vast majority of insect pollination in the Galapagos (Linsley 1966, Linsley et al. 1966, McMullen 1985,
1989, Phillip et al. 2006, Chamorro et al. 2012). As a dominant and keystone pollinator, negative impacts on its populations may have significant effects on the plant-pollinator networks of the islands.

Eradication of established non-native populations is costly and rarely successful (Mack et al. 2000), and control policies seem to be effective only before species are widespread (Olson et al. 2012; Pitt et al. 2012). In this context, the Agency for Regulation and Control of Biosecurity and Quarantine for Galapagos (ABG) plays a decisive role in preventing new introductions of non-native amphibians, reptiles and birds in Galapagos, especially hitchhikers. Furthermore, for already established non-native species, it is important to stop new or multiple introductions of the same species, since they will increase reproductive output and genetic diversity (Lambrinos 2004; Van Wilgen & Richardson 2012). Quarantine officers should pay particular attention to horticultural trade and temperature-controlled freights because their constant temperatures make them non-lethal to amphibians and reptiles (Work et al. 2005). Decks and exposed cargo on boats are another facilitator of non-native species, especially hitchhikers with larger sized bodies, such as snakes, iguanas and birds.

If the eradication of non-native established species is of interest, the eradication programme of Columba livia is a successful but rather unique story (Phillips et al. 2012b). The success was due, in part, to the availability of good and updated knowledge about the species’ natural history, distribution, ecological relationships, effects and eradication methods (Phillips et al. 2012b). In contrast, eradication attempts of other non-native species that are less well researched have been unsuccessful (e.g., Scinax quinquenectiatus\textsuperscript{34}).

\textsuperscript{34} Eradication attempts by hand-capture, spraying caffeine and increasing the salinity of the lagoons were unsuccessful (Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012).
Very little information has been published about the natural history of most non-native amphibians, reptiles and birds in their native distribution in mainland Ecuador. Knowledge on non-native species is paramount to knowing whether controlling them should be a conservation goal in the archipelago and, if so, how such an objective can be best achieved. Even the species identity of some species is uncertain (e.g., *Rhinella horribilis*, *Scinax quinquefasciatus*, and *Lampropeltis micropholis*). Furthermore, knowledge about Galapagos populations remains, in many cases, unpublished. Most terrestrial non-native hitchhikers in the Galapagos are geckos and their effects on Galapagos biodiversity have been usually considered as low or absent. Unfortunately, Marinus Hoogmoed’s (1989) words are remain valid in these cases: “these are only speculations based on few observations”. With all these restrictions, control policies are not sufficiently evidence-based. Future research on non-native species should provide information on habitat and microhabitat use, physiology and growth, intra-population tolerance to abiotic and biotic factors, reproductive biology and population dynamics, as well as diet and trophic interactions, both in Galapagos and in their native distributions.

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35 For example, available knowledge for the populations of *Scinax quinquefasciatus* in Galapagos remains in two unpublished dissertations: Pazmiño (2011) described the genetic diversity and origin of the Galapagos populations of *S. quinquefasciatus* and Vintimilla (2005) analysed the control potential from increasing water salinity.
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## Appendices

### Appendix 1 List of dispersing species of amphibians, reptiles and birds in the Galapagos Islands

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<th>Biogeographic Origin</th>
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<td>Hitchiker</td>
<td>Baltra</td>
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Appendix 2 Accounts of dispersing species of amphibians in Galapagos

Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a) reported a Western Cane Toad *Rhinella horribilis* on Galapagos (as *Bufo* sp. and *Chaunus marinus*, respectively). Records at the Vertebrate Collection of the Charles Darwin Research Foundation (VCCDRS; CDF 2016) show that it was discovered in a house at Puerto Baquerizo Moreno, San Cristóbal Island, on 5 February 1995. This species has a large native range from the southern United States to the lowlands of western Ecuador and northwestern Peru (Frost 2016). It inhabits a large variety of ecosystems and is abundant in anthropogenic areas like pastures and gardens (Zug and Zug 1979). Although it can live in arid environments, it depends on water availability for reproduction (see Zug and Zug 1979 for information on its natural history). *Rhinella horribilis* is present in Manta, Guayaquil and Tababela (Quito), which are areas with cargo warehouses, maritime ports and airports with connections to Galapagos (pers. obs.). Apparently, only one population of *Rhinella horribilis* may have established itself completely outside of its native range (in Florida, King and Krakauer 1966; Easteal 1981). No information is available on potential or evidenced impacts by non-native *R. horribilis*. Comparatively, the Eastern Cane Toad *Rhinella marina* has been successfully introduced around the world (Easteal 1981; Lever 2003), and is one of the most studied introduced species, especially in Australia. The main evidenced ecological impact of *R. marina* is

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36 The correct updated name of the toad that arrived to the Galapagos is *Rhinella horribilis*, assuming its origin was western Ecuador. Until recently, *R. horribilis* was a synonym of *Rhinella marina*. However, Acevedo-Rincón et al. (2016) recognised them as different species. *Rhinella marina* is now restricted to the east of the Andes. Further taxonomic changes are expected, and populations from western Ecuador could receive yet another (new) name (Vallinoto et al. 2010).

37 The non-native populations of *Rhinella* in Florida have multiple origins, with first individuals coming from Surinam and Colombia. Toads from Surinam were probably *Rhinella marina*, while those from Colombia could be *R. horribilis* if their origin was western Colombia or *R. marina* if they came from eastern Colombia.
the decline of Australian native predators, due to its toxicity when ingested (Shine 2010).

Snell (2000) reported an individual **Striped Robber Frog** *Pristimantis unistrigatus* beside a dishwasher in a house on 17 March 2000 in Puerto Ayora, Santa Cruz Island. Phillips et al. (2012a) reported another *P. unistrigatus* on Isabela Island, but did not provide further details. There are no specimens of *Pristimantis* at the VCCDRS. Frogs of the genus *Pristimantis* are part of the superfamily Brachycephaloidea (Frost 2016). Brachycephaloidean frogs are terrestrial breeders, laying their eggs on land with no need of water. Their eggs hatch directly into froglets, bypassing the tadpole stage. These features could provide clear advantages to establishing self-sufficient populations in islands with limited freshwater availability. Frogs of the Brachycephaloidean genus *Eleutherodactylus* have established spreading populations in Hawaiian and Caribbean islands, where they arrived as hitchhikers (Kraus et al. 1999; Kraus and Campbell 2002; Lever 2003; Olson et al. 2012). However, introduced populations of *Pristimantis* are undocumented (Lever 2003, Kraus 2009), probably because most *Pristimantis* show high levels of endemism and high physiological specialisation. Nevertheless, a few species, like *P. unistrigatus*, are more widespread and have adapted to human-created habitats, showing potential to establish non-native populations if the conditions for establishment are adequate. *Pristimantis unistrigatus* is native to inter-Andean highland valleys from southern Colombia to central Ecuador, where it can live in mildly arid environments with seasonal rains and thrive in agricultural lands, gardens and other artificially watered areas (Lynch 1981). It is the most common frog in urban, suburban and rural green areas of the valley of Quito, including the surroundings of air cargo warehouses and the airport (pers. obs.).
**Fowler's Snouted Treefrog Scinax quinquefasciatus**[^38][^39] is the only amphibian established in the Galapagos. Snell et al. (1999) and Snell and Rea (1999) published the first reports of *S. quinquefasciatus* from Galapagos based on records from Isabela[^40] and Santa Cruz islands. Although subsequent authors have commented on *S. quinquefasciatus* in Galapagos (Lever 2003; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a; Zug 2013), many details about their introduction history remain unpublished. The VCCDRS (CDF 2016) holds several specimens of *S. quinquefasciatus* that offer valuable information to better contextualize its timeframe in the archipelago. The first specimen of *S. quinquefasciatus* (VCCDRS 2247) was collected on May 1973 at an unknown locality on Santa Cruz Island. Four additional specimens were collected in 1991–1992 in the dry lowlands of Santa Cruz Island, in urban areas of the town of Puerto Ayora. Between 1998 and 2013, one to four specimens were obtained in or around Puerto Ayora every year, except for 2011, when 10 specimens were collected. In 2001, the first *S. quinquefasciatus* (VCCDRS 1502) was collected at humid highlands in agricultural areas of Bellavista, Santa Cruz Island, with additional single treefrogs collected in 2003, 2008, 2011 and 2013. Seven treefrogs were collected in 2000 and one in 2001 in the dry lowlands of urban Puerto Baquerizo Moreno, San Cristobal Island. No further records have been reported since[^41]. All six VCCDRS specimens of *S. quinquefasciatus* from Isabela Island were collected after its confirmed establishment at the lagoons near the town of Puerto Villamil in 1998. Since *S. quinquefasciatus* is

[^38]: This name is currently applied to different populations of *Scinax* that include at least one undescribed cryptic species (R.W. McDiarmid in litt. 2003; S. Ron pers. comm. 2013).

[^39]: The Global Invasive Species Database (GISD 2010) erroneously reported *Eleutherodactylus coqui* as being found in Galapagos, citing Snell and Rea (1999) as the source, yet those authors reported *Scinax quinquefasciatus*.

[^40]: Snell and Rea (1999) confused specimens from Isabela with “leptodactylid frogs”, a common error due to the snout form and general appearance of *Scinax* frogs.

[^41]: Phillips et al. (2012) reported a “Tree frog 3 (*Hyla* sp.)” reported from San Cristobal in 1990. It is possible that it corresponds to early records of *Scinax quinquefasciatus*. Due to uncertainty with the identification and lack of voucher specimens, they are not included in these analyses.
insectivorous, predation on native invertebrate fauna has been identified as a potential impact on Galapagos biodiversity (Phillips et al. 2012a), but there are no studies regarding its diet or evidence about any real impact. *Scinax quinquefasciatus* is native to the Pacific lowlands and low montane areas from southwestern Colombia to central-western Ecuador (Frost 2016). In its native distribution, *S. quinquefasciatus* occurs in a variety of habitats, as it is able to breed in small ponds in agricultural areas, herbaceous marshes and stream pools in arid zones and wetlands with low salinity in river deltas (Duellman 1971; de la Riva et al. 1997; Cisneros-Heredia 2006a; Ortega-Andrade et al. 2010; pers. obs.). It is present in urban, suburban and green rural areas of Manta and Guayaquil, including the surroundings of air cargo warehouses and the airport (pers. obs.).
Appendix 3 Accounts of dispersing species of reptiles in Galapagos

Dwarf Gecko *Gonatodes caudiscutatus*\(^{42}\) is found in small numbers in the town of Puerto Baquerizo Moreno\(^{43}\), San Cristobal Island, where it is restricted to moist anthropic environments. It is abundant in the agro-urban highlands of San Cristobal in El Progreso, where it has also been able to establish itself in natural areas (Garman 1892; Wood 1939; Mertens 1963; Wright 1983; Hoogmoed 1989; Lundh 1998; Olmedo and Cayot 1994; pers. obs.). During a survey in June 2009, I found three specimens of *G. caudiscutatus* in gardens near Playa Man and near the interpretation centre as well as 10 specimens at orchards in El Progreso. The rarity of *G. caudiscutatus* in the lowlands is probably due to climate restrictions and predation by domestic and native species\(^{44}\) (Wright 1983; Hoogmoed 1989; Olmedo and Cayot 1994; pers. obs.). There are reports of *G. caudiscutatus* on at least two other islands of Galapagos. Jimenez-Uzc特别gui et al. (2007) reported it on Baltra, without further details. The VCCDRS (CDF 2016) has four specimens of *G. caudiscutatus* collected in Puerto Ayora, Santa Cruz Island on 5 November 2003, 29 January 2006 and 20 July 2006. It is probable that a small population has already established itself on Santa Cruz Island. Impacts by *G. caudiscutatus* on Galapagos biodiversity are unknown, but have been suspected to be slight or even non-existent (Hoogmoed 1989; Olmedo and Cayot 1994; Phillips et al. 2012a). Competition or exclusion of endemic geckos is unlikely, due to body size, habitat and

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\(^{42}\) Garman (1892) described *Gonatodes collaris*, based on two specimens collected by George Baur at Wreck Bay, next to the town of Puerto Baquerizo Moreno, San Cristobal Island. Vanzolini (1965) proposed that *G. collaris* and *G. caudiscutatus* were actually synonyms, which was later confirmed by Wright (1983).

\(^{43}\) Several expeditions did not find *Gonatodes* on San Cristobal Island during the late 1800s and early 1900s (Cope 1889; Heller 1903; Van Denburgh 1912; Slevin 1935). Van Denburgh (1912), Slevin (1935) and Barbour and Loveridge (1929) suggested that the specimens reported by Garman (1892) were probably collected at Guayaquil, in mainland Ecuador. However, it is probable that *G. caudiscutatus* was overlooked due to its restricted distribution and low abundance in Puerto Baquerizo Moreno and low activity during the dry season.

\(^{44}\) I observed the San Cristobal Lava Lizard *Microlophus bivittatus* predating on *G. caudiscutatus* on June 2005. See account of Domestic Chicken *Gallus gallus* for details on a predation event on *G. caudiscutatus*. 
microhabitat differences\textsuperscript{45}. Although \textit{G. caudiscutatus} is insectivorous, it probably eats mainly non-native and widespread invertebrates, but there are no studies about its diet. \textit{Gonatodes caudiscutatus} are native to the lowlands of central-western Ecuador and extreme northwestern Peru (Sturaro and Avilá-Pires 2014). They are present in urban, suburban and green rural areas of Guayaquil, including the surroundings of air cargo warehouses and the airport (pers. obs.).

\textbf{Peters' Leaf-toed Gecko \textit{Phyllodactylus reissii}} arrived to Santa Cruz Island in the mid-1970s (Wright 1983, Hoogmoed 1989, Olmedo and Cayot 1994). Hoogmoed (1989) published a detailed study on the population in Puerto Ayora, where it was well established in the urban area (Hoogmoed 1989, Olmedo and Cayot 1994). Olmedo and Cayot (1994) reported one individual of \textit{P. reissii} in natural areas next to Puerto Ayora (adjacent to Las Ninfas neighbourhood). On July 1997, I observed three \textit{P. reissii} in the same area in natural vegetation. \textit{Phyllodactylus reissii} has reached the highlands of Santa Cruz Island, at Bellavista (Phillips et al. 2012a). Torres-Carvajal and Tapia (2011) reported the first record of \textit{P. reissii} at Puerto Villamil, Isabela Island, but the presence of an established population remains to be confirmed. During a survey in June 2009, I did not find \textit{P. reissii} on San Cristobal Island, but in July 2017 it was found in El Jardín de las Opuntias, a natural area in the lowlands of San Cristobal. \textit{Phyllodactylus reissii} inhabits dry forests and scrubland, and rural, suburban and urban areas from central western Ecuador to northwestern Peru (Dixon and Huey 1970). In Galapagos, \textit{P. reissi} remains mostly restricted to urban, suburban and rural areas, although it is present in natural areas in the lowlands. In areas of Puerto Ayora where \textit{P. reissii} is

\textsuperscript{45} All endemic Galapagos geckos belong to the genus \textit{Phyllodactylus}, are diurnal and nocturnal and inhabit the arid lowlands. They are scansorial and arboreal, having dorsoventrally compressed digits with greatly expanded lamellae. \textit{Gonatodes caudiscutatus} have a smaller body-size than all endemic geckos, are diurnal and mainly inhabit the humid highlands. They are terrestrial and semi-arboreal, having more restricted climbing abilities than the endemic geckos due to their cylindrical digits without expanded lamellae.
dominant, it appears to have displaced the endemic *P. galapagensis*; they rarely cohabitate the same areas (Hoogmoed 1989; Olmedo and Cayot 1994). No information about possible exclusion mechanisms or interactions has been published\(^{46}\). In natural areas in the lowlands, *P. reissii* may impact endemic *Phyllodactylus* through competition (Hoogmoed 1989; Olmedo and Cayot 1994; Phillips et al. 2012a).

**Mourning Gecko *Lepidodactylus lugubris*** is native to Southeast Asia and the islands of western Oceania (Hoogmoed and Avila-Pires 2015 and citations therein). It is a parthenogenetic species, which benefits the establishment of new populations (Kraus 2009; Phillips et al. 2012a; Hoogmoed and Avila-Pires 2015). It has become established in north-eastern Asia, the west coast of South America, Oceania and Pacific Ocean islands, including Galapagos (Lever 2003; Kraus 2009; Hoogmoed and Avila-Pires 2015). *Lepidodactylus lugubris* likely arrived to Galapagos during the early 1980s\(^{47}\) (Hoogmoed 1989; Olmedo and Cayot 1994). It remained rare during the first decade\(^{48}\), but subsequently became well established and dispersed. Nowadays, it has fairly large self-sustaining populations, but only in moist environments in coastal areas (i.e., artificially watered urban areas and mangroves) in the towns of Puerto Ayora, Puerto Baquerizo Moreno and Puerto Villamil (Olmedo and Cayot 1994; Sengoku 1998; Jiménez-Uzcátegui et al. 2007, 2015; Torres-Carvajal and Tapia 2011; Phillips et al. 2012a; pers. obs.). It has also established itself in the town of El Progreso, where it remains restricted to human buildings and has not been found on farms (M. Altamirano, in litt. 12 June 2009). Jiménez-Uzcátegui

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\(^{46}\) At least one study on interactions between non-native and endemic geckos in Galapagos has been conducted but remains unpublished (M. Altamirano’s PhD dissertation, cited by Phillips et al. 2012).

\(^{47}\) Hoogmoed (1989) published the first mention of *Lepidodactylus lugubris* in Galapagos. However, he did not find the species, and cited the unpublished records obtained by John Wright at Puerto Ayora, Santa Cruz Island, in 1983.

\(^{48}\) Marinus Hoogmoed did not find *Lepidoblepharis lugubris* during his intensive surveys of Puerto Ayora in 1988 (Hoogmoed 1989; Lundh 1998).
et al. (2015) reported *L. lugubris* from Marchena Island, without further details. The consequences of the introduction of *L. lugubris* in Neotropical areas, including Galapagos, are unclear (Hoogmoed and Avila-Pires 2015). No impacts on Galapagos’ biodiversity have been reported (Olmedo and Cayot 1994; Phillips et al. 2012). Competitive interactions between *L. lugubris* and Galapagos endemic geckos have apparently not affected endemic species (M. Altamirano 2002 cited in Phillips et al. 2012a). Although *L. lugubris* is insectivorous, it probably eats mainly non-native and widespread invertebrates. There are no studies yet about its diet.

**Common House Gecko *Hemidactylus frenatus*** is a nocturnal species native to southeastern Asia (Lever 2003). It has invaded several areas across the planet, including many islands in the Indian and Pacific oceans and several areas of Africa and America. It currently has the widest worldwide non-native distribution of its genus (Lever 2003; Kraus 2009). Torres-Carvajal and Tapia (2011) reported the first record of *H. frenatus* in Galapagos, based on five individuals found at Puerto Villamil, Isabela Island, but an established population was not confirmed. On 24 October 2016, three *H. frenatus* were recorded at Puerto Villamil, thus suggesting that an established population is indeed present on Isabela Island (T. Schramer and Y. Kalki, in litt. 2016). It seems to have also established itself in Puerto Baquerizo Moreno, San Cristobal Island, where over 10 individuals were recorded between September and November 2016 in human buildings (T. Schramer and Y. Kalki, in litt. 2016). Due to its recent arrival, no information is available for any type of interactions or effects of *H. frenatus* on the endemic *Phyllodactylus* geckos. However, its arrival has raised concerns due to reported impacts on native fauna in other areas where it has established itself (Torres-Carvajal and Tapia 2011; Torres-Carvajal 2015). *Hemidactylus frenatus* has outcompeted and excluded non-native *Lepidodactylus lugubris* from several Pacific islands by competitive exclusion (Petren and Case 1998; Kraus 2009). Preliminary evidence suggests that *H. frenatus* may be also excluding *L. lugubris* in San Cristobal (T. Schramer and Y. Kalki, in litt. 2016). On the Mascarene Islands,
*H. frenatus* contributed to the decline and population extirpation of endemic geckos of the genus *Nactus* (Cole et al. 2005). Furthermore, it could carry novel parasites that might impact native reptile species (Hoskin 2011).

On 22 February 2014, a local inhabitant ran over a **Milksnake Lampropeltis micropholis** in the area of Santa Rosa, highlands of Santa Cruz Island. Photographs of the snake were quickly disseminated through social networks and Galapagos authorities were able to recover the specimen. Four days later, the specimen was delivered and deposited at the Laboratory of Terrestrial Zoology, Universidad San Francisco de Quito (USFQ), by officials of the Ministry of Environment of Ecuador (MAE) in order to confirm its identification and preserve it as a voucher specimen. Morphology and colouration data suggest that the specimen belongs to the population distributed in the Pacific lowlands of Ecuador. In mainland Ecuador, *L. micropholis* inhabits the Pacific lowlands and Andean highlands in a large variety of ecosystems, from arid to moist habitats (Cisneros-Heredia and Touzet 2007). *Lampropeltis micropholis* is present in the surroundings of Guayaquil and Quito (Williams 1988; Pérez-Santos and Moreno 1991; Cisneros-Heredia and Touzet 2007). This snake is terrestrial, active during day and night, and eats a large variety of vertebrates and invertebrates (Williams 1988). There are no records of non-native populations of *L. micropholis*

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49 Until recently, *Lampropeltis micropholis* was a subspecies of *L. triangulum*. However, Ruane et al. (2014) raised it to species status. As currently understood, *L. micropholis* occurs from western Costa Rica to Ecuador. Further taxonomic changes are expected and populations from the highlands of Ecuador could receive yet another (new) name (J. Valencia, in litt. 2012).

50 *Lampropeltis micropholis* is rather frequent in the highlands, even in rural and suburban areas. However, there are few specimens from the lowlands (Cisneros-Heredia and Touzet 2007; pers. obs.). Williams (1988) reported it from Guayaquil, based on a specimen collected by Edward Whimper during the 1890s. Perez-Santos and Moreno (1991) reported the species from the province of Guayas, without providing details. Although no further information about *L. micropholis* from Guayaquil has been published, I am aware of two additional records: One individual collected ca. 18 km from Guayaquil and delivered it to Jean-Marc Touzet (Fundación Herpetológica “Gustavo Orcés” FHGO) in February 1990 (Touzet JM pers. comm.) and another was photographed by Keyko Cruz at Cerro Blanco, ca. 8 km from Guayaquil (Cruz 2015).
established outside of its range, or studies of insular populations. For comparison, a study of the diet of insular populations of *Lampropeltis polizona* on Isabel Island, Mexico, showed that they fed on different species of terrestrial lizards and nestlings of ground-nesting marine birds, including Blue-Footed Booby *Sula nebouxii*, but avoided arboreal geckos and tree-nesting birds. The California Kingsnake *Lampropeltis californiae* became established in Gran Canaria Island, where its main evidenced ecological impact is predation on endemic lizards (Pether and Mateo 2007; Cabrera-Pérez et al. 2012).

Several individuals of **Green Iguana** *Iguana iguana* have reached the Galapagos Islands (Cruz Martínez et al. 2007; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a). Five specimens are deposited at the VCCDRS (CDF 2016). The earliest *I. iguana* (VCCDRS 571) was collected on 15 February 1982 at an unknown locality in Santa Cruz Island. Two additional specimens were found at a private house in the town of Puerto Ayora, Santa Cruz Island, on 14 August 200051 (CDF 2016). One *I. iguana* (VCCDRS 2218) was found at an unknown locality on San Cristobal Island, on 19 April 2008; while another (VCCDRS 2153) was found in Isabela Island on 14 June 2010 (CDF 2016). Cruz Martínez et al. (2007) and Phillips et al. (2012a) mentioned an *I. iguana* found walking in the streets of Puerto Baquerizo Moreno, San Cristobal Island. Another was photographed on a dock at Puerto Ayora on 13 August 2015 (Christen 2015). *Iguana iguana* is native from Mexico to Paraguay and southern Brazil (Uetz and Hošek 2016). It is very common in the littoral and lowlands of western Ecuador (Ortega-Andrade et al. 2010), including the surroundings of cargo warehouses and the air and maritime ports of Guayaquil (Cruz Martínez et al. 2007; pers. obs.). *Iguana iguana* is able to disperse between islands by ocean rafting (Censky et al. 1998). However, I agree with Jiménez-Uzcátegui et al. (2007, 2015) and Phillips et al. (2012a) in classifying it as a non-

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51 However, Jiménez-Uzcátegui et al. (2007) reported that only one *Iguana iguana* was found in Santa Cruz in 2000, while the other was found in San Cristobal.
native introduced species, as there is evidence of its hitchhiking behaviour (Cruz Martínez et al. 2007). In some islands where it has been introduced, *I. iguana* has displaced the native *I. delicatissima* by hybridisation (Lever 2003; Powell and Henderson 2005; Kraus 2009; Powell et al. 2011; Vuillaume et al. 2015). Since inter-generic hybridisation has been reported in iguanas (Rassmann et al. 1997; Jančúchová-Lásková et al. 2015), the establishment of *I. iguana* in Galapagos could pose a threat for the endemic iguanas of the genus *Amblyrhynchus* and *Conolophus*.

One Yellow-Footed Tortoise *Chelonoidis denticulata* on Santa Cruz Island, one Yellow-Spotted River Tortoise *Podocnemis unifilis* on San Cristobal Island and a single Common Slider Turtle *Trachemys scripta* on Santa Cruz and San Cristobal islands were intercepted (Jiménez-Uzcátegui et al. 2007, 2015; Phillips et al. 2012a). All individuals were apparently brought to Galapagos as pets, and these three species are commonly traded as pets in mainland Ecuador (Carr and Almendáriz 1989; Cisneros-Heredia 2006b; pers. obs.). *Chelonoidis denticulata* and *P. unifilis* are native to the Amazonian lowlands. They are illegally caught and occasionally sold in pet stores of Quito and Guayaquil (pers. obs.). *Trachemys scripta* is native to the western United States and Mexico and it is the most common pet turtle and the most widely released reptile species in the world (Kraus 2009).

A gravid **Five-Lined Skink Plestiodon inexpectatus** was intercepted as a pet in Galapagos. Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a) cited the island of interception as San Cristobal. However, VCCDRS data indicate that it was intercepted at the Baltra airport on 26 May 2005 (CDF 2016).
Appendix 4 Accounts of dispersing species of birds in Galapagos

Domestic ducks\textsuperscript{52}, Domestic Turkey \textit{Meleagris gallopavo}, Domestic Goose \textit{Anser anser}, Domestic Quail \textit{Coturnix japonica}\textsuperscript{53}, Domestic Guineafowl \textit{Numida meleagris} and Green Peafowl \textit{Pavo muticus} occur in the Galapagos only in agro-urban areas under human care (Gottdenker et al. 2005; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a). None of them have established self-sustaining populations outside of farms. The 2014 Census of Agricultural Production (CGREG 2014) reported 926 ducks and 28 turkeys, all free-range on Santa Cruz, San Cristobal and Isabela islands (Appendix 4). While the number of turkeys declined by one-third when compared with the census of 2000, the population of ducks increased by 117% (CGREG 2014).

\textbf{Domestic Fowl or Chicken} \textit{Gallus gallus} has been introduced across the planet as domestic poultry, with over 21 billion reported in 2014 (FAO 2015). Several populations have become feral, especially in the Pacific islands, including Galapagos (Phillips et al. 2012a; McGowan and Kirwan 2016). The 2014 Census of Agricultural Production (CGREG 2014) reported that 22,180 free-range and 70,750 intensive poultry chickens were in Galapagos. Domestic Chickens are found on all four inhabited islands of Galapagos: Santa Cruz, San Cristobal, Floreana and Isabela (Appendix 4). While Floreana Island has the largest number per inhabitant and the greatest density in agricultural lands of free-range chicken, San Cristobal and Santa Cruz are the islands with the greatest density of free-range chickens (Appendix 4). Vargas and Bensted-Smith (2000), Gottdenker et al. (2005), Wiedenfield (2006) and Phillips et al. (2012a) reported feral (or semi-feral) populations of chickens established on

\textsuperscript{52} Domestic ducks in Galapagos seem to be a mix of descendants from the Mallard \textit{Anas platyrhynchos} and the Muscovy Duck \textit{Cairina moschata}.

\textsuperscript{53} Japanese Quail \textit{Coturnix japonica} and Common Quail \textit{C. coturnix} are distinct but closely related species (Johnsgard 1988; McGowan and Kirwan 2016). \textit{Coturnix japonica} was domesticated in eastern Asia several centuries ago, and domesticated quails are derived from \textit{C. japonica} and its hybrids with \textit{C. coturnix} (Guyomarc’h 2003). While \textit{C. coturnix} is a partially migratory species, the domestic \textit{C. japonica} lost its migratory impulse during domestication (Derégnaucourt et al., 2005; Guyomarc’h, 2003).
the four inhabited islands. However, it remains unclear if those populations are indeed self-sufficient and truly feral (i.e., completely independent of human care).

The main potential impact of Domestic Chicken on native fauna is the spreading of infectious diseases to native birds (Wikelski et al. 2004; Gottdenker et al. 2005; Hernandez-Divers et al. 2008; Soos et al. 2008; GISD 2010; Deem et al. 2012). Yet, this threat has not been demonstrated and the evidence remains theoretical and correlative (GISD 2010; Baker et al. 2014). The Global Invasive Species Database (GISD 2010) mentions that G. gallus could negatively impact native vertebrates, but their only reference (Varnham, 2006) is anecdotal and based on a different species (Green Junglefowl Gallus varius). Phillips et al. (2012) noted: “no impacts [by G. gallus] to the [Galapagos] native biota have been documented”.

I present here the first evidence of predation on squamate reptiles by Domestic Chickens in Galapagos. In June 2009, I observed a hen attacking a small Galapagos Racer Pseudalsophis biserialis in a private yard next to the road between Puerto Baquerizo Moreno and El Progreso, San Cristobal Island. The hen pecked on the snake’s head and body, after which it seized the snake with its beak and started to run, chased by another hen. Eventually, the hens carrying the snake took cover inside a shed. In July 2009, I observed a hen chasing a small Dwarf Gecko Gonatodes caudiscutatus, apparently found while foraging among some leaf litter and rocks in a private yard at El Progreso, San Cristobal Island. The gecko managed to flee and hide under rocks. In July 1997, I observed a rooster pecking and eating a dead Peters' Leaf-toed Gecko Phyllodactylus reissi in a vacant urban lot at Santa Cruz Island.

Gallus gallus mainly eats seeds and other plant material, although it is an omnivorous bird. Red Junglefowl, the wild ancestor of the Domestic Chicken, occasionally eats lizards and snakes (Ali and Ripley 1980). Reports of attacks and predation on squamate reptiles by Domestic Chicken are rare occur
worldwide (Guthrie 1932, Bell 1996; Powell and Henderson 2008; Mesquita et al. 2009; Sasa et al. 2009; pers. obs.). Scarcity of records would suggest that chicken predation on lizards and snakes is an opportunistic yet atypical behaviour. However, it could also be due to under-reporting and paucity of herpetologists surveying chicken yards. Free-range chickens can move over hundreds of meters away from their shelters to forage, usually towards hedges and borders where encounters with small snakes and lizards would be more prone to occur, though they would remain unwitnessed.

Four **Domestic Pigeon** *Columba livia* were brought to Floreana Island during the early 1970s to establish a dovecote (Harmon et al. 1987). Within the next decade, pigeons were introduced to Santa Cruz, San Cristobal and Isabela islands (Harmon et al. 1987). The population increased rapidly, and ca. 550 pigeons were present in Galapagos by 2001 — most of them semi-feral or feral (Phillips et al. 2003). The main potential impact of Domestic Pigeon on Galapagos fauna was the spreading of the protozoan parasite *Trichomonas gallinae* to the endemic Galapagos Dove *Zenaida galapagoensis* (Harmon et al. 1987; Phillips et al. 2003). Indirect evidence for this threat was anecdotal and correlative, based on the presence of the parasite *Z. galapagoensis* on islands where pigeons occurred (and their absence on pigeon-free islands) and the decline of *Z. galapagoensis* on islands populated by pigeons (Baker et al. 2014; Wikelski et al. 2004). In 2000, on the basis of the precautionary principle, Galapagos National Park Service and Charles Darwin Research Station started an eradication program of *Columba livia* (Phillips et al. 2012b). *Columba livia* was declared eradicated from Galapagos in 2007 (Phillips et al. 2012b).

**Red-Masked Parakeet** *Psittacara erythrogenys* was reported on Puerto Baquerizo Moreno, San Cristobal Island, in April 1996 (Vargas 1996, as *Aratinga erythrogenys*). Vargas (1996) obtained reports from local inhabitants of the presence of two or three parakeets. He also observed one *P. erythrogenys* flying between the town and the surrounding natural areas. These parakeets were possibly escaped pets and probably did not establish themselves there;
no sightings of these birds they have not been reported since (Wiedenfeld 2006; Phillips et al. 2012a). *Pssitacara erythrogenys* is endemic to central-western Ecuador and south-western Peru, where it inhabits deciduous and semi-deciduous forests (Ridgely and Greenfield 2001). It is among the most common birds illegally caught and traded (Juniper and Parr 1998), and freed pets can be found almost anywhere in Ecuador (pers. obs.). There are self-sustained non-native populations of *P. erythrogenys* in Spain and the United States.

**Smooth-billed Ani *Crotophaga ani*** naturally\(^{54}\) expanded its distribution from South America to southern Florida, the Caribbean and Central America during the 20th century (Terborgh and Faaborg 1973; Terborgh et al. 1978; Quinn and Startek-Foote 2000; Payne and Kirwan 2016). Humans apparently introduced *C. ani* to the Galapagos Islands as a possible biological control against ticks (Harris 1973; Grant and Grant 1997; Phillips et al. 2012a)\(^{55}\). The first records of *C. ani* in Galapagos were in 1962, on Isabela Island. It progressively expanded to all major islands of the archipelago (Harris 1973; Grant and Grant 1997; Wiedenfeld 2006; Connett et al. 2013). At present, the estimated population of *C. ani* in Galapagos is over 250,000 individuals (Connett et al. 2013). *Crotophaga ani* is mainly insectivorous, but it also consumes plant material (especially fruits) and vertebrates (including lizards, snakes, frogs, birds and mice) (Bent 1940; Skutch 1959; Olivares and Munves 1973; Rosenberg et al. 1990; Burger and Gochfeld 2001; Payne and Sorensen 2005; Repenning et al. 2009; Connett et al. 2013). Predation on animal material seems to increase during the breeding period, which coincides with the wet season when *C. ani* apparently prefers grasshoppers and other orthopterans

\(^{54}\) *Crotophaga ani* expansion across America has not been mediated by humans. The species is not listed within the GISD (2010).

\(^{55}\) Still, this introduction hypothesis remains an assumption, mainly based on the apparently low capacity of anis to self-disperse through long distances across oceans (Harris 1973; Grant and Grant 1997; Phillips et al. 2012).
Hymenopteran insects, such as euglossine bees and social wasps *Polystes* spp., have been reported as part of the diet of *Crotophaga ani* (Skutch 1959; Rosenberg et al. 1990; Raw 1997; Burger and Gochfeld 2001; Repenning et al. 2009). Two studies on the diet of *C. ani* on Santa Cruz Island showed the presence of hymenopterans. Rosenberg et al. (1990) reported hymenopterans in only 4 of 24 dissected gizzards. Connett et al. (2013) found 12 *X. darwini* in the gizzards of 12 *C. ani*, but, in this case, it was the single most frequent invertebrate species.

Four potential impacts by *Crotophaga ani* on Galapagos biodiversity have been postulated (Rosenberg et al. 1990; Grant and Grant 1997, Dvorak et al. 2004; Fessl et al. 2010):

(i) Propagation of invasive plants. Available evidence suggests that *Crotophaga ani* has a high potential to propagate introduced plants, including the invasive Raspberry *Rubus niveus* and Wild-Sage *Lantana camara* (Guerrero and Tye 2011).

(ii) Predation on native fauna. Rosenberg et al. (1990), Guerrero and Tye (2011), and Connett et al. (2013) reported predation of Galapagos native invertebrates, lizards and Darwin Finch nestlings by *Crotophaga ani*.

(iii) Competition with native avifauna, which remains untested and speculative.

(iv) Introduction of avian diseases, also untested and speculative.

Nonetheless, Phillips et al. (2012a; contra Rosenberg et al. 1990) stated that the Smooth-Billed *Ani* is “a low priority alien species, not having been attributed with any serious impacts to native species, although it is likely that it has some effects on native [fauna]”.

I present herein information that constitutes the first evidence of a probable major impact on an endemic invertebrate due to predation by *Crotophaga ani*.

Between 8 and 16 June 2009, I observed six groups of *C. ani* predating
assiduously on Galapagos Carpenter Bee *Xylophaga darwini* at six different locations on San Cristobal Island. Carpenter bees in high densities were foraging on blooming trees in the Dry Zone, usually near the coast. I observed one group of *C. ani* over a 30-minute period and the other five groups during 15-minute periods each. In total, the six groups consumed 661 bees over the observation periods. Each bird captured an average of 8.5±4.4 (range = 4–15) bees per 15 minutes. *Crotophaga ani* continued preying upon bees after each observation period ended. Despite the continuous attacks, the bees did not disperse and more kept arriving, as they were attracted by the flowers. Although large numbers of the non-native Social Wasp *Polistes versicolor* as well as some butterflies were also present, *C. ani* largely ignored them.

An individual of Saffron Finch *Sicalis flaveola* was intercepted in 2014 at Baltra Island’s airport, where it arrived as a hitchhiker on an airplane from Quito (Jiménez-Uzcátegui et al. 2015). Interestingly, after its interception, it was returned to Quito where local staff misidentified it as a Galapagos endemic bird and sent it back to the archipelago56 (Jiménez-Uzcátegui et al. 2015). In Ecuador, *S. flaveola’s* native distribution is in arid semi-open areas with scattered trees or shrubs and agricultural areas of south-western Ecuador, both lowlands and inter-Andean highland valleys (Ridgely and Greenfield 2001). During the 21st century, *S. flaveola* started to expand along the central-western lowlands and northern inter-Andean highland valleys of Ecuador (Henry 2005; Buitrón and Freile 2006; Cisneros-Heredia et al. 2015). It is now a frequent species in the valley of Quito, including the surroundings of air cargo warehouses and the airport (Cisneros-Heredia et al. 2015; pers. obs.).

Phillips et al. (2012a) and Jiménez-Uzcátegui et al. (2015) reported an individual of Great-Tailed Grackle *Quiscalus mexicanus* captured in the

56 When it arrived to Galapagos for the second time, it was weak and died by the next day (Jiménez-Uzcátegui et al. 2015)
town of Puerto Ayora, Santa Cruz Island in 2010. However, there is a previous record of this grackle that remained unreported: One *Q. mexicanus* was filmed at Santa Cruz Island on May 2005. *Quiscalus mexicanus* has a broad distribution, from central USA to the Pacific coasts of Ecuador and northern Peru (Fraga 2014). It has considerably expanded its distribution through the northern United States and Caribbean islands (Dinsmore and Dinsmore 1993; Wehtje 2003; Fraga 2016). *Quiscalus mexicanus* was first reported from the Caribbean islands in the mid-2000s (Mejía et al. 2009; Paulino et al. 2013; Levy 2015). Currently, it seems to be established at least in Jamaica and Hispaniola (Paulino et al. 2013; Levy 2015). Grackles have been observed to hitchhike on passenger boats (Norton 1902), and Haynes-Sutton et al. (2010) mentioned that *Q. mexicanus* probably reached Jamaica with cargo. The paucity of records of *Q. mexicanus* in islands suggests that it is a poor disperser across oceanic barriers, but cargo and passenger boats may offer aid for oceanic trips. The same transport mechanism was probably used by *Q. mexicanus* to reach Galapagos (although this remains an assumption). Thus, I include this species as a non-native introduced species, rather than as a vagrant.

**Pied-billed Grebe Podilymbus podiceps** was first recorded in 1960 in wetlands at Santa Cruz Island. To date, single individuals and pairs have been continuously recorded during every month at least since the late 1990s on Isabela, Santa Cruz, Floreana and San Cristobal islands. Records in the wetlands near Puerto Villamil, Isabela Island are increasingly common. Castro and Phillips (1996) reported sightings of immature specimens on San Cristobal and Die (2017) reported a pair displaying. Abundance of records in recent years is probably also influenced by increased number of birdwatcher tourists and by facilities provided by citizen-science initiatives such as eBird to access observation records. Continuous records across all months in 2016-2017 suggest that the species is not a migrant, as stated by Wiedenfeld (2006). Instead, *P. podiceps* seems to have small populations, which probably breed in Galapagos.
Black-bellied Whistling-Duck *Dendrocygna autumnalis* is a vagrant with two records in Galapagos: at Puerto Villamil, Isabela Island, on 2 July 1960 and at Puerto Ayora, Santa Cruz Island, on 25 October 1999 (Wiedenfeld 2006).

**Masked Duck** *Nomonyx dominicus* has been recorded at least four times in Galapagos: A pair with a duckling at El Junco lagoon, San Cristobal Island, December 1994; a male on a marshy pond in the highlands of Santa Cruz Island, 28 July 1999; an adult female on a large pond in Punta Moreno, Isabela Island, 08 June 2001; and one sight record at El Chato lagoon, Santa Cruz Island, 22 August 2003 (Stotz 1999; Die 2001; Wiedenfeld 2006).

**Snowy Egret** *Egretta thula* was first recorded in Galapagos in 1965. Subsequently, several records have been reported from most large islands of Galapagos (Wiedenfeld 2016; pers. obs. at El Junco lagoon [July 2009] and Wreck Bay [July 2017], San Cristobal Island). Although usually single individuals have been observed, a flock of up to 20 individuals was reported flying to roost on Santa Cruz lagoons (Mina & Woodward 2015). The species is not a vagrant as stated by Wiedenfeld (2006). Instead, *E. thula* seems to have small populations and most probably breeds in Galapagos.

**Little Blue Heron** *Egretta caerulea* has been recorded at least eight times in Galapagos: an individual (white juvenile molting to adult plumage) at the mangroves in Elizabeth Bay, Isabela Island, on 10 December 1997; a second sighting at the same location on 18 November 1998; a sighting at the lagoons of Barrio Estrada, Puerto Ayora, Santa Cruz Island, on 25 May 1999; an immature specimen at Punta Espinoza, Fernandina Island, on 01 April 2011; an adult at the Charles Darwin Research Station beach, Santa Cruz Island, on 19 April 2012; a white juvenile at Punta Cormoran, Floreana Island, on 10 July 2013; one sighting at Playa de Los Perros, Santa Cruz Island, on 15 August 2014; one sighting at Puerto Ayora, Santa Cruz Island, on 09 May 2015; an adult at a dock in Puerto Ayora, Santa Cruz Island, on 28 March 2017.
Tricolored Egret *Egretta tricolor* has been reported only three times in Galapagos: a record by Swash and Still (2000) without any details, another one apparently from Santa Cruz in 2011 and the only one with details in Darwin Bay, Genovesa Island, in 2014 (Wiedenfeld, 2006; Jiménez-Uzcátegui et al., 2017).

Cattle Egret *Bubulcus ibis* was first recorded in Galapagos on 2 November 1964 on Santa Cruz Island, but the species may have arrived earlier (Wiedenfeld 2006; Lévêque et al., 2016). Currently, it has breeding colonies on the main islands and is widespread across the archipelago (Wiedenfeld 2006).

*Bubulcus ibis* has been commonly identified as a non-native invasive species on the Galapagos Islands. However, its arrival to the Galapagos was not human-mediated, but was rather a natural colonisation based entirely on the species’ adaptations to successfully disperse across oceanic routes. The original distribution of *B. ibis* included the south of the Iberian Peninsula and parts of sub-Saharan and meridional Africa. During the 19th century, *B. ibis* underwent an enormous expansion, and it has currently colonized all continents except Antarctica (Martínez-Vilalta and Motis 1992; Martínez et al. 2017). Its natural arrival to Galapagos was a matter of time and its establishment would have happened with or without anthropic areas, since it may inhabit swamps and mangroves. The existence of agricultural areas in Galapagos only facilitated the expansion of populations of *B. ibis* to additional areas of the archipelago. Its situation is very similar to *Neocrex erythrops*, also a recent arrival that has benefited from agricultural and other anthropic areas.

Paint-Billed Crake *Neocrex erythrops* was first recorded in Galapagos in 1953, but it is possible that it was previously overlooked (Wiedenfeld 2006). It has been recorded in Santa Cruz, San Cristobal, Isabela, Floreana and Genovesa.
islands. Nesting populations occur in Santa Cruz, Floreana, San Cristobal and (probably) Isabela islands.

**Purple Gallinule *Porphyrio martinicus*** was reported as having “long periods of residence, bordering on being a permanent resident in recent years” (Wiedenfeld 2006), but nevertheless it was classified as vagrant (Wiedenfeld 2006). It has been recorded on Santa Cruz, Española, San Cristobal and Isabela island, although no breeding events have been recorded.

**Eared Dove *Zenaida auriculata*** has been reported few times in Galapagos: on Champion Islet, in August 1980; in Los Gemelos, Santa Cruz Island, on 13 September 1983; at the Charles Darwin Research Station, Puerto Ayora, Santa Cruz Island, on 29 January 1984 and 10 August 1985; and five individuals were observed at the airport on Baltra Island, on 15 December 2012 (Curry and Stoleson 1988; Wiedenfeld, 2006; Loranger, 2012). Although most records are in urban areas, their origin cannot be directly assigned to hitchhiking since this species is capable of oceanic dispersing (Baptista et al. 2013).

**Grey-Capped Cuckoo *Coccyzus lansbergi*** was reported by Ridgely and Greenfield (2001) as a vagrant in Galapagos, but they did not provide any further information. At best, it was an irregular vagrant.

**Brown-hested Martin *Progne tapera*** was recently reported by Jiménez-Uzcátegui et al. (2017) on Española Island based on records by Sean M. Williams and E. H. Burtt, but without further information.

**Bananaquit *Coereba flaveola*** was reported by Swash and Still (2000), but without any further information.