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Modelling the effects of agriculturalisation on faunal ecosystem service provision and demand in the tropics

Gutierrez Arellano, Claudia

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Modelling the effects of agriculturalisation on faunal ecosystem service provision and demand in the tropics

Claudia Renata Gutierrez Arellano

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Department of Geography
King's College London

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Abstract

Land use and cover change (LUCC) is considered one of the main drivers of biodiversity loss and deterioration of ecosystem services (ES) globally. Currently, the highest land conversion is occurring in tropical regions from forest to agricultural land, i.e. agriculturalisation. Tropical forests contain the highest biodiversity on Earth and are recognised as highly relevant for ES provision.

Fauna provides key regulating services (e.g. pollination, natural pest and disease control and long-distance seed dispersal) the so-called faunal ecosystem services (FES). This research aimed to assess how agriculturalisation affects the distribution of FES provision and demand at pantropical scale. For this it was necessary:

a) To identify FES with potential to be spatially modelled through a comprehensive literature review, which summarises the importance of animal populations as providers of regulating ecosystem services and the identified consequences of agriculturalisation on animal populations.

b) To generate a spatial model of FES provision and demand pantropically. A pantropical pollination model was generated by combining previously suggested models with novel variables and methods, using geographic information system techniques.

c) To use a LUCC model to generate projections of future agriculturalisation in tropical regions under two scenarios of change: a conservation scenario, where deforestation is restricted to occur outside protected areas; and a non-conservation scenario, where deforestation can occur within protected areas. Constant deforestation rates were assumed for both scenarios.

d) To use the land-use change projections to model pollination service under these scenarios and quantify the changes in provision and demand due to conversion of forest to cropland.

The main findings of this research are:

- Abundance and capacity of movement of providers are highly relevant for the occurrence of some FES (i.e. pollination, natural control, seed dispersal) and determines the spatial distribution of the service. However, this could vary among ecosystem services and is context-dependent.
- The agriculturalization of forested areas can increase the service provision by wild bees in the short term. However, deforestation and cropland expansion could have a negative impact on pollination service pantropically in the long term.
- A decrease in current deforestation rates, an increase in forest protection and incorporation of natural habitats in agricultural landscapes are necessary to maintain current pollination service through time.

Enhancement of FES can have positive effects on agroecosystems, by increasing productivity and food security, and on natural systems, by reducing the pressure of agriculturalisation on both, provider and non-provider populations.

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1 Introduction

1.1. Rationale

Tropical forests harbour the highest biodiversity on Earth and are where the greatest habitat loss is occurring due to land use and cover change from forest to agricultural land (Lambin et al. 2003). Land-use and cover change (LUCC) is considered one of the main drivers of biodiversity loss and deterioration of ecosystem services (ES, Foley et al. 2005, Newbold et al. 2015).

Over the past 60 years, anthropogenic disturbance has changed natural environments at a rate and extent that is unprecedented during human history (MA 2005). This has led to a global loss of biodiversity, which has been compared to mass extinction events that have occurred periodically throughout the history of Earth (Barnosky et al. 2011, Ceballos et al. 2015) and has put the provision of ecosystem services in jeopardy (Foley et al. 2005).

For thousands of years, humans have obtained essential ecosystem services –such as food, freshwater and shelter–through diverse and low-intensity land-use practices. Some of these practices have led to the degradation of ecosystems and the services they provide. Over 60% of ES assessed by the Millennium Ecosystem Assessment (15 out of 24) are deteriorating or already overused worldwide, including 70% of regulating and cultural services (MA 2005).

1.2. Biodiversity and ecosystem services

Variation of biotic elements at all organizational levels, number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits, and landscape units in a given system, constitute biodiversity (Díaz et al. 2006, Cimon-Morin et al. 2013). Biodiversity is recognized as the main factor to sustain the stability of life on Earth (CBD 2000) and plays an essential and complex role in all levels of ES production (Pimentel et al. 1997, Balvanera et al. 2006, Mace et al. 2012).

The importance of the natural environment for the survival of humanity has been recognized from ancient times (Fisher et al. 2009). However, the conception of the term “ecosystem service” goes back only a few decades. From its first appearance in the book of Ehrlich and Ehrlich (1982) up to now, the use of the term has increased exponentially in the context of scientific research (Fisher et al. 2009). This is because of the need to understand the role of ES in human well-being, the complexity of its production and maintenance and the attempt to reduce its loss and degradation (Daily 1997, Boyd and Banzhaf 2007).

One of the simplest and commonly cited definitions is “the benefits people obtain from ecosystems” (MA 2005). However, given the evolution of the conceptual framework, higher accuracy has been proposed. Boyd and Banzhaf (2007) define ES as “final components of nature, directly enjoyed, consumed, or used to yield human well-being”. In this definition, ES are limited to final ecosystem components and ecosystem processes are excluded. However, there are ecosystem processes (also referred to as functions) that ultimately give rise to goods and benefits for humans(e.g. pollination give rise to food production). Wallace (2007) and Fisher et al. (2009) support the recognition of ecosystem processes as services along with their final benefits to carrying out proper management of ES. Under this approach, processes can be the objective of conservation and management to secure final benefits.

Accurate definition and characterisation are essential to properly manage, valuate and conserve ES. Although considerable advances have been made, there is still a need to improve the theoretical framework for ES assessment. Currently, The Common International Classification for Ecosystem Services (CICES, Haines-Young and Potschin-Young 2018) includes both processes and final services. These are grouped into three main categories: a) provisioning of material and energy needs (e.g. food, fibre), b) regulation and maintenance of the environment for humans (e.g. air quality regulation, pollination), and c) cultural significance, i.e. the non-material characteristics of ecosystems that affect physical and mental states of people (e.g. recreation, spiritual experience). These, in turn, are divided into biotic and abiotic, depending on the service provider.

Identifying ecosystem service providers and characterising their functional relationships are among the key research areas to increase understanding of ES production (Kremen 2005). Luck et al. (2003) suggest the term service-providing unit for those biological entities – populations, species, functional group, etc. –that provide ES. The delineation of the service-provider unit varies depending on the considered service and any temporal or spatial variation characteristic of the provider in question and the service itself (Kremen 2005, Harrison et al. 2014).

Biodiversity loss threatens ES provision and therefore, human well-being (Díaz et al. 2006). The importance of biodiversity in underpinning some ecosystem processes and delivering ES is well known (Mace et al. 2012, Bastian 2013). Recently, several studies about the role of biodiversity in maintaining ES have increased the understanding of the biodiversity-ES relationship (Harrison et al. 2014). However, ecosystem functions and ES delivery involve intricate ecological interactions (Kremen et al. 2007, Duncan et al. 2015). Despite the intrinsic value of biodiversity for ecosystems (i.e. organisms have an unquantifiable and untransactable value), presence of biodiversity and ES supply are not synonyms. The relationship between biodiversity and ES is complex. There is still much to know and understand about the linkages between different biodiversity components and ES production (Duncan et al. 2015), such as species richness (number of species), abundance (number of individuals of a species), functional diversity or evenness (similarity among the number of individuals of different species in a community). This is particularly true for many ecosystem services provided by mobile organisms (Jonsson et al. 2014), these include some ES provided by animals, i.e. faunal ecosystem service (FES).

The effect of LUCC on FES provision has been scarcely studied and mostly limited to case studies. Here is presented an initial assessment on the role of regulating FES to croplands and the potential effects of agriculturalisation on provision (i.e. service is provided but not necessarily consumed) and demand (i.e. service currently consumed or used in a certain area over a given time, Burkhard et al. 2012) for FES across the tropics using a modelling approach.

The main outcomes of this research are: a spatially explicit model of a FES, insect pollination by wild bees, at pantropical scale, which allows identification of where in the tropical regions is the highest service provision and demand; the implementation of this model to assess current status of protection of suitable habitat for wild bees; and a quantitative assessment on the potential changes in this service due to agriculturalisation at regional and pantropical scales. These outcomes were used as a baseline to analyse the feasibility of generating models for other FES (natural pest control and seed dispersal) and to assess the implication of LUCC pantropically.

1.3. Aim and objectives

1.3.1. Aim

This thesis aims to assess how LUCC (in particular from forest to cropland) impacts the distribution of FES supply, as a result of the interaction of habitat loss and degradation affecting FES providers, i.e. animal populations. We begin by assessing pollination services supply by wild insects and demand as determined by land use of insect-pollinated crops.

FES providers

To achieve this aim, there are two main topics to address. The first topic relates to FES providers and FES spatial distribution. Providers are a key element to understand ES provision (Harrison et al. 2014). The **initial questions** raised were:

What animal taxa have a direct relationship with the production of regulating ES?

What are the most relevant factors that influence richness, abundance and distribution of FES providers in the tropics?

What are the possible approaches to model the spatial distribution of FES providers?

Impact of habitat loss on FES providers

Having identified key FES providers and influential factors in their distribution, it is possible to address the second main topic, the possible effects on FES providers of habitat loss and degradation due to agriculturalisation, in terms of both FES supply and demand.

Impact on FES supply and demand

The knowledge generated from answering the previous questions helps to answer the main research questions:

1. Do habitat loss and degradation due to land-use conversion from forest to cropland have an impact on FES provision?
2. How does agriculturalisation affect the distribution of FES provision and demand in tropical forests and in agricultural land near forests?
3. What are the possible impacts on FES supply and demand under different scenarios of land-use change from forest to cropland in the tropics?

1.3.2. Objectives

The objectives to answer these questions and to achieve the research aim are:

Objective 1. To identify faunal ecosystem services with the potential to be spatially modelled

To understand the effect of land-use change on FES, first, it is necessary to gather the evidence that shows where strong links exist between fauna and to regulating ES provision. After identifying and describing those services, the relationship between agriculturalisation and FES provision and demand must be assessed. A spatial model will be generated from the FES identified as having a strong relationship with agriculturalisation.

Objective 2. To generate a pantropical spatial distribution model of a faunal ecosystem service provision and demand

Once a FES has been selected, the modelling of the potential distribution involves two main tasks. First, to identify the most relevant variables that explain the occurrence of FES providers at the relevant geographical scale (i.e. pantropically); and second, to determine the modelling approach, considering previously trialled and novel methods. This model aims to evaluate the potential (i.e. provision) and realised (i.e. demand) distribution of the selected services throughout the study area.

Objective 3. To generate projections of land use and cover change from forest to cropland at pantropical scale

This objective is focused on developing projections of deforestation where forest is replaced by cropland under two scenarios of change considering business as usual trends (i.e. current deforestation trends are maintained over time): a) a “conservation” scenario, where deforestation allocation excludes protected land, and b) a “non-conservation” scenario, where deforestation also occurs in protected land. These scenarios are simulated as both short and long term.

Given the diversity of existing datasets and land-use change models, a selection of a spatially explicit model that accurately reflects the pattern and process of change for the entire study area must be carried out. The use of the land-use change model aims to identify geographical patterns of change (i.e. where deforestation is more likely to occur) considering current deforestation rates since the progression of those into the future is unknown and dependent upon economy and technology.

Objective 4. To quantify changes in FES supply and demand due to land-use change under different scenarios of conversion

LUCC projections are incorporated as scenarios to the FES model to obtain the potential distribution of services under different scenarios. Thus, it is possible to estimate the changes in provision and demand of FES between present day (baseline) and future scenarios and between conservation and non-conservation scenarios. This is estimated in terms of gain and/or loss of service provision relative to the baseline considering the percentage of forest cover change through time.

1.4. Thesis overview

The content of this thesis comprises six chapters:

Chapter 1.

This chapter includes a brief introduction to the research problem and rationale and describes the aim and objectives. Broad definitions of biodiversity, ES and LUCC are provided, and the FES concept is introduced. The relationship between LUCC and biodiversity and ES loss is briefly explained. The main components of the research are described, research questions are listed, and the main objectives are explained. Finally, an overview of the thesis chapters is provided.

Chapter 2.

This chapter is a scoping review article that compiles evidence on the effects of agriculturalisation on FES provision. In the initial section of the article, regulating services provided by fauna: animal pollination, biological control of crop pests and human diseases and seed dispersal are defined. The main providers are identified and evidence supporting the strong direct relationship between animal populations and service production is summarised. Next, the role of species richness and abundance in FES provision is addressed. The following section explains how FES providers can also be a source of *disservices* in relation to agriculturalisation and describes the impacts of invasive species, the spread of human diseases, and crop pests and raiding.

The following sections focus on the effects of agriculturalisation on FES providers due to landscape homogenisation and fragmentation, habitat loss, microclimatic changes, pest proliferation and use of chemical pest control. Once the effects are identified, the negative impacts on FES production as a consequence of loss of species richness and decrease in population abundance are described. Final sections focus on the potential changes to regulating FES supply and demand under future agriculturalisation and the expected global demand for regulation FES.

Chapter 3.

This chapter is presented as a research article and is focused on the development of a pantropical model of service provision and demand. The selected service is animal pollination, an essential ecosystem function to sustain wild plant communities and tropical crops. Wild bees are the selected providers given the major contribution of this group to this FES. The sections of this chapter are structured into two main topics: 1) generation of the pantropical pollination model and 2) implementation of the model to quantify the current status of the service throughout tropical forests and within tropical protected areas.

First, the data and methods applied to derive the variables used to generate a spatially explicit probabilistic model of pantropical potential and realised pollination are described. Second, improvements, limitations and possible applications of this model are discussed in this chapter. Finally, the role of protected forest in the conservation of pollination service and the relevance of pollination service in biodiversity conservation strategies are discussed.

Chapter 4.

The effects of agriculturalisation on the spatial and temporal distribution and quantity of potential and realised pollination services are assessed in this chapter using a LUCC model. First, the land use and land cover concepts are described along with the historical causes of LUCC in tropical forests. Then a brief introduction to spatial LUCC models for tropical regions and LUCC scenarios is presented. This is followed by a description of the LUCC model, scenarios of change and approach used to incorporate projections of future agriculturalisation into the model presented in Chapter 3.

A quantitative analysis of change in potential and realised pollination services is presented first at regionals scale—five regions across the tropical forests of the world— and then pantropically. A current (baseline) scenario is compared with two future scenarios of provision in the short term (32 years) and long term (200 years). Differences and similarities between scenarios and among regions and further research opportunities are discussed.

Chapter 5.

The potential to develop a pantropical natural pest control model and a pantropical seed dispersal model is addressed in this chapter. For each of these FES, the ecological knowledge that has allowed the generation of spatial models is summarised, followed by a brief description of the methods and main outcomes of such models. The opportunities, challenges and considerations of using these approaches, along with the suggestion of alternative indicators to generate pantropical models for these FES is assessed.

Chapter 6.

This chapter comprises the main conclusions of this research. It summarises the answers for the research questions raised in Chapter 1, describes the achievements of the proposed objectives and the main findings of Chapters 2-4. Finally, the areas of further research identified in Chapters 2-5 are mentioned.

2 Faunal ecosystem services and agriculturalisation: a scoping review

2.1. Introduction

A scoping review was carried out to map the relevant literature on the main topic ‘Effects of agriculturalisation on regulating ES provided by fauna’. This chapter presents a published review paper (Gutierrez-Arellano and Mulligan 2018) on this subject. First, the evidence on the regulating FES is presented and complemented with evidence on disservices provided by fauna in the context of agriculturalisation, i.e. the functions that directly or indirectly undermine human-wellbeing (Shackleton et al. 2016). Second, the evidence on the consequences of agriculturalisation on service providers is linked with their effect on the provision.

The current information on the possible state of provision and demand for regulating FES under future agriculturalisation is summarised at the end of the paper. Finally, the conclusions of this review describe the current research gaps and possible approaches to enhance the knowledge of the subjects covered.

2.2. A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision, globally

Nature Conservation 30: 1–39 (2018)
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REVIEW ARTICLE

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A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision, globally

Claudia Gutierrez-Arellano[1], Mark Mulligan[1]

[1] *Department of Geography, King's College London, 30 Aldwych, London WC2B 4BG, UK*

Corresponding author: *Claudia Gutierrez-Arellano* (claudia.gutierrez_arellano@kcl.ac.uk)

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Abstract

Land use and cover change (LUCC) is the main cause of natural ecosystem degradation and biodiversity loss and can cause a decrease in ecosystem service provision. Animal populations are providers of some key regulation services: pollination, pest and disease control and seed dispersal, the so-called faunal ecosystem services (FES). Here we aim to give an overview on the current and future status of regulation FES in response to change from original habitat to agricultural land globally. FES are much more tightly linked to wildlife populations and biodiversity than are most ecosystem services, whose determinants are largely climatic and related to vegetation structure. Degradation of ecosystems by land use change thus has much more potential to affect FES. In this scoping review, we summarise the main findings showing the importance of animal populations as FES providers and as a source of ecosystem disservices; underlying causes of agriculturalisation impacts on FES and the potential condition of FES under future LUCC in relation to the expected demand for FES globally. Overall, studies support a positive relationship between FES provision and animal species richness and abundance. Agriculturalisation has negative effects on FES providers due to landscape homogenisation, habitat fragmentation and loss, microclimatic changes and development of population imbalance, causing species and population losses of key fauna, reducing services whilst enhancing disservices. Since evidence suggests an increase in FES demand worldwide is required to support increased farming, it is imperative to improve the understanding of agriculturalisation on FES supply and distribution. Spatial conservation prioritisation must factor in faunal ecosystem functions as the most biodiversity-relevant of all ecosystem services and that which most closely links sites of service provision of conservation value with nearby sites of service use to provide ecosystem services of agricultural and economic value.

Keywords
crop raiding, disease control, providers, invasive species, pest control, pollination, seed dispersal

Introduction

Biodiversity is recognised as a key support for stable life on Earth (Hautier et al. 2015) and plays an essential and complex role in all levels of ecosystem services production (Pimentel et al. 1997, Balvanera et al. 2006, Mace et al. 2012). To properly manage, value and conserve ecosystem services (ES), it is essential to have an accurate definition and characterisation of the services and the traits that underpin them. Ecosystem service providers are the species or entities on which the service provision depends and identifying and characterising their functional relationships are amongst the key research areas to increase understanding of the link between biodiversity and ecosystem services production (Luck et al. 2003, Kremen 2005, Duncan et al. 2015).

Animals are key ecosystem services providers; therefore, we denominate faunal ecosystem services (FES) as those services that rely heavily on animal population. Fauna is a source of provisioning (e.g. Henchion et al. 2014), cultural (e.g. Villamagna et al. 2014) and regulation (e.g. Kremen et al. 2007) services. For the latter, animals perform functions that allow ecosystem maintenance and thus production of other services, such as food or fibre provision. Conserving animal populations that provide FES is essential to maintain the correct functioning of ecosystems to provide ecosystem services where there is demand for them.

An imbalance of animal populations may be the cause of reduced FES production and/or the generation of faunal ecosystem disservices, such as the occurrence of crop pests (e.g. Rasmussen et al. 2017) and the spread of zoonotic diseases to humans (e.g. McCauley et al. 2015). Evidence suggests that such an imbalance can result from land use and cover change (LUCC), the dominant form of which globally is agriculturalisation of natural ecosystems (e.g. Wilby and Thomas 2002, McCauley et al. 2015). LUCC is considered the most important driving force of biodiversity and ecosystem function loss (MA 2005, Bastian 2013).

Regulation FES occur mostly at the local scale (Kremen et al. 2007) and the assessment of their provision and effects of LUCC has been evaluated at this scale (e.g. Kremen et al. 2002, Levey et al. 2008, Chaplin-Kramer et al. 2011). Although many studies have focused on finding spatial congruence between faunal diversity and regulation ecosystem services at large scales (Naidoo et al. 2008, Luck et al. 2009), these studies assess groups unlikely to produce a direct influence on the regulation services, e.g. linking diversity of vertebrates to carbon storage (Strassburg et al. 2010) or threatened species to freshwater provision (Larsen et al. 2011). This research is limited to describing spatial patterns of biodiversity and ecosystem services but does not assess the underlying role of faunal diversity in providing regulation ecosystem services. The direct relationship between animal diversity and regulation FES beyond the local scale and understanding the effects of LUCC on FES provision globally remains to be evaluated.

In this scoping review, we aim to give an overview of the current and future situation of regulation FES in response to agriculturalisation globally. We summarise the most relevant evidence addressing the following topics: a) the relevance of animal populations as providers of regulation services; b) the role of species richness and of abundance of providers in regulation FES provision; c) animal populations as a source of ecosystem disservices, d) the effects of agriculturalisation on FES providers, e) the mechanisms underlying the observed negative impact of provider loss on regulation FES provision, f) the potential condition of regulation FES under future LUCC and g) the expected demand of regulation FES worldwide.

Rationale

First, we summarise the evidence available to support the FES concept, which highlights animal populations as essential providers of animal pollination, biological control (including pest and disease control) and seed dispersal, as fundamental regulation services operating in both natural ecosystems and agriculture. Hereafter, the topics included in the review are addressed per service, in the order given.

ES provision has been used as a strong argument for biodiversity conservation (e.g. Balmford et al. 2002, Balvanera et al. 2006, Cardinale et al. 2011, Bastian 2013) and, simultaneously, this idea has been widely debated (e.g. Schwartz et al. 2000, Balvanera et al. 2001, Kleijn et al. 2015). Ecosystem services are by definition a function of supply and demand (there is no service without demand for it) and for many services proximity to demand is key. Many non-FES services are as much a function of climate, landscape and ecosystem structure as they are of biodiversity or species abundance. We give an overview of the role of richness and abundance in regulation FES provision to assess if FES provision can more directly support faunal conservation than other types of ecosystem service provision.

This is followed by the evidence showing the negative impacts on human well-being that can be produced by animal populations under agriculturalisation, which are referred to as faunal ecosystem disservices (Lyytimäki and Sipilä 2009, Shackleton et al. 2016). Like all the components of ecosystems, animal populations can be a source of benefit or can undermine human well-being (Zhang et al. 2007, von Döhren and Haase 2015; Figure 1). It has been recognised that the occurrence of services and disservices is part of a continuum and must be examined together to improve the understanding of their relationship with biodiversity (Shackleton et al. 2016). We address the faunal disservices caused by both invasive and native species including spread of human diseases, crop pests and crop raiding.

Finally, we synthesise evidence indicating the causes of loss of FES providers in response to the consequences of agriculturalisation: landscape homogenisation, habitat fragmentation and loss, microclimatic changes, proliferation of pests and use of pesticides. We describe the impacts of loss of FES providers on provision. It is worth mentioning that we make a distinction between the effects on providers and on provision because the former indicates the causes of loss and the latter its consequences.

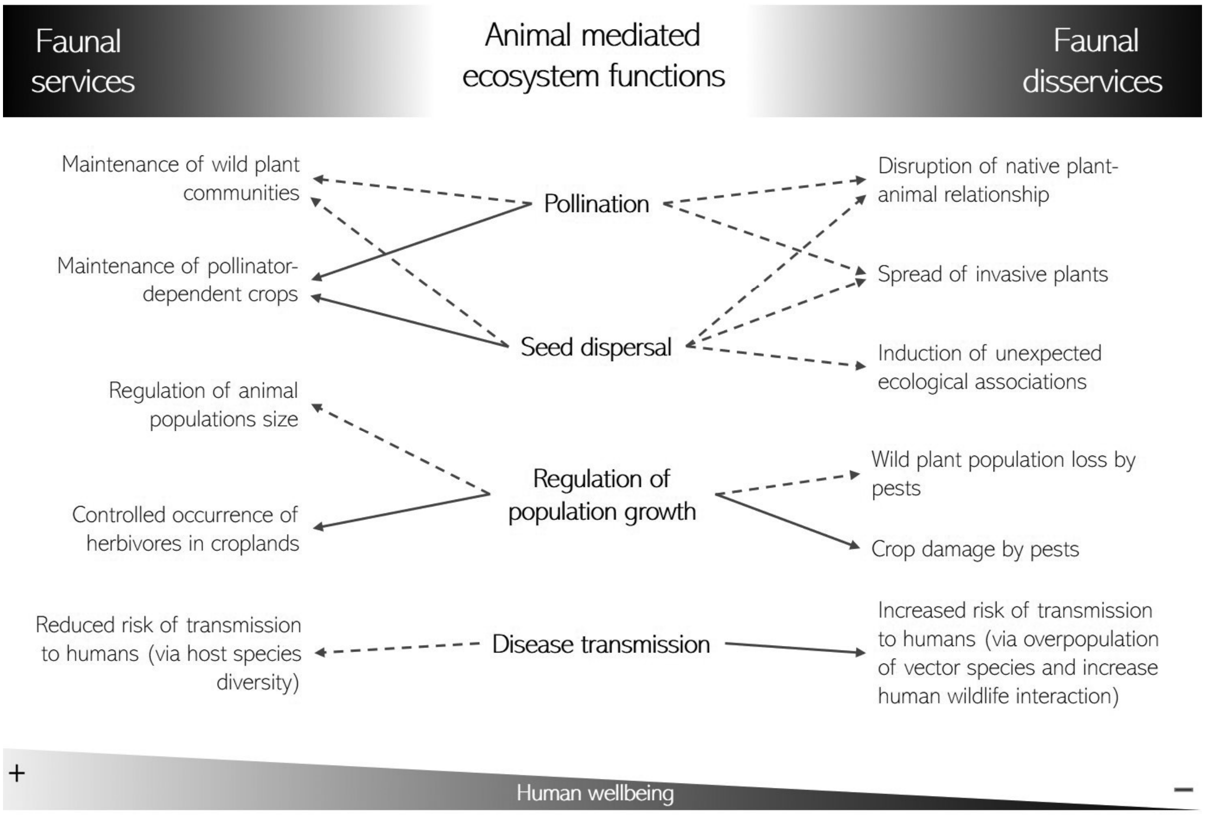

Figure 1. Animal populations as source of services and disservices. The same ecosystem function mediated by animal populations may enhance (faunal service) or undermine (faunal disservice) human well-being and it can manifest directly (solid arrows) or indirectly (dashed arrows).

Having addressed the present situation of FES and impacts of agriculturalisation, we address the potential trajectories for FES in the future based on the few studies that have used modelling to project agriculturalisation over the next decades and which have also assessed the impact on regulation services. Finally, we assess the expected demand for FES worldwide, given projected population growth and agricultural expansion since service provision cannot be assessed unless changes in demand are understood.

Regulation faunal ecosystem services

Ecosystem functions can produce ecosystem services (benefits or goods) where there is human demand. A key suite of these services are the regulation services (Haines-Young and Potschin 2011). Animal populations are essential providers of the following regulation services: 1) animal pollination, for which insects, especially bees, are the major providers (e.g. Kremen et al. 2002, Klein et al. 2007); 2) natural pest control, provided mainly by vertebrate predators (e.g. Mols and Visser 2007, Maas et al. 2016) and parasitoid invertebrates (e.g. Letourneau et al. 2015); 3) human disease control provided by vertebrates (e.g. tick-borne diseases, Ostfeld and LoGiudice 2003, McCauley et al. 2015); and 4) seed dispersal, where providers are mostly birds and flying mammals (e.g. McConkey and Drake 2006, García and Martínez 2012).

The assessment of regulation FES provision is complex, since populations of providers form intricate ecological relationships (e.g. Perfecto and Vandermeer 2006). It requires identification of the community structure that influences ecosystem function and assessment of the key factors affecting such provision, along with the spatial and temporal scale at which providers and services operate (Kremen 2005). FES providers can include a single population (e.g. Hougner et al. 2006), multilevel taxonomic groups (e.g. Blanche and Cunningham 2005, Maas et al. 2013) and different functional groups (e.g. Letourneau et al. 2015). Since service provision assumes a demand for the service, we must also understand the drivers and spatial distribution of that demand.

Most studies in which animal pollination and biological control are evaluated have been carried out in agroecosystems (Table 1), due to the relevance of these FES on crop yield, food supply and the role of providers in agricultural economy (Ricketts et al. 2004, Blanche and Cunningham 2005, Morandin and Winston 2006), while seed dispersal has been evaluated mostly in natural ecosystems, where it is fundamental to understand plant community composition (Wenny et al. 2016). These studies have been carried out throughout the world, mostly at the local scale.

There is a wide range of measures used to assess FES provider contributions to different services (Table 1) and methods vary from purely observational (i.e. natural conditions, e.g. McConkey and Drake 2006) or experimental (i.e. controlled conditions, e.g. Maas et al. 2013, Garratt et al. 2016) to a combination of both (e.g. Hougner et al. 2006, Egerer et al. 2018). Below, we summarise the evidence per service, showing the relevance of animals as FES providers.

Animal pollination

Animal pollination is a fundamental process in terrestrial ecosystems and is essential for maintenance of wild plant communities and agricultural systems (Potts et al. 2010). Faunal pollination is a key ecosystem service in agricultural productivity. In contrast with the other regulation FES, the contribution of animal pollination has been widely quantified.

According to Klein et al. (2007), 35% of crops depend on pollinators globally, while Kremen et al. (2002) estimated 66% for the 1,500 crop species of the world amounting to between 15 and 30% of food production. Williams (1996) estimated for European crops that over 80% of the 264 species assessed require animal pollination. Roubik (1995) estimated that productivity of approximately 70% of tropical crops is improved by animal pollinators. Regarding wild plant species, 80% of flowering plants are directly dependent on insect pollination for fruit and seed set globally (Klein et al. 2007, Ollerton et al. 2011).

Given the morphological diversity of plants, the degree of self-compatibility and the diversity of reproductive organs in the flowers of crops, a great diversity of vectors is required for efficient animal pollination (Williams 2002, Blüthgen and Klein 2011). Insects are the most important animal pollinators by virtue of their abundance and foraging behaviour (Williams 2002). Thousands of species of bees, flies, wasps, beetles,

Table 1. Faunal ecosystem services. Selected examples of studies where regulation ecosystem services provided by fauna are assessed, describing the providers, ecosystem benefited by the service and service quantification measure.

Ecosystem service	Service provider	Ecosystem	Measure	Study site	Reference
Pollination	Native bees	Agroecosystem (watermelon crops)	Pollen deposition	Yolo County, California, USA	Kremen et al. (2002)
	Exotic and native bees	Agroecosystem (coffee plantation)	Seed mass, fruit set, peaberry frequency, pollen deposition, bee species richness	Finca Santa Fe, Valle General, Costa Rica	Ricketts et al. (2004)
	Nitidulid and Staphylinid beetles	Agroecosystem (atemoya crops)	Beetle species richness	Atherton Tableland, Queensland, Australia	Blanche and Cunningham (2005)
	Wild bees	Agroecosystem (canola crops)	Bee abundance, seed set	La Crete, Alberta, Canada	Morandin and Winston (2006)
	Ceratopogonids midges	Agroecosystem (cocoa and plantain crops)	Midges abundance, pod set, intercropping proportion	Kubease, Abrafo-Ebekawopa and Edwenease, Ghana	Frimpong et al. (2011)
	Hoverfly, solitary mason bee and bumblebee	Agroecosystem (apple orchards)	Flower visitation, fruit set	Reading and Leeds experimental farms, UK	Garratt et al. (2016)
Pest control	Parasitoid eggs (Mirid bug, Wolf spider, Tetragnathid spiders)	Agroecosystem (rice crops)	Plant- and leaf-hoppers abundance	Luzon, Ifugao, Philippines	Drechsler and Settele (2001)
	Aztec ant and Green scale (mutualism avoids occurrence of coffee berry borer)	Agroecosystem (coffee plantation)	Ant activity, green scales abundance	Finca Irlanda, Chiapas, Mexico	Perfecto and Vandermeer (2006)
	Great Tits	Agroecosystem (apple orchards)	Percentage of caterpillar damage per apple tree	Netherlands	Mols and Visser (2007)
	Birds and bats	Agroecosystem (cacao plantations)	Herbivorous insect abundance, final crop yield	Napu Valley, Central Sulawesi, Indonesia	Maas et al. (2013)
	Birds and bats	Agroecosystem (coffee plantation)	Herbivorous arthropod abundance and leaf damage proportion	Finca San Antonio and Hacienda Rio Negro, Coto Brus Valley, Costa Rica	Karp and Daily (2014)
	Parasitoid wasps and flies	Agroecosystem (cruciferous crops)	Parasitoid richness, abundance of parasitised cabbage by aphids and loopers	Monterey, Santa Cruz, and San Benito Counties, California, USA	Letourneau et al. (2015)
	Leaf beetles, root and flower-feeding weevils	Wetland	Purple loosestrife cover, occurrence of feeding damage and abundance of biological control agents	Minnesota, USA	Wilson et al. (2004)
Human diseases control	Mammals, birds and reptiles	Temperate forest	Infected ticks with Lyme disease proportion	Southern New York State, USA	Ostfeld and LoGiudice (2003)
	Birds	Forested urban to rural areas	Bird diversity, mosquitoes and humans infected West Nile virus	St Tammany Parish, Louisiana, USA Ozark forest, Missouri, USA	Ezenwa et al. (2006)Allan et al. (2009)

Ecosystem service	Service provider	Ecosystem	Measure	Study site	Reference
Human diseases control	Small wild mammals	Desert (Caatinga) Tropical forest (Amazon) Wetland (Pantanal)	Small mammal diversity and abundance, dogs infected with Chagas disease	Amazon Basin, Brasil	Xavier et al. (2012)
	Rodents	Evergreen forest and Agroecosystem (mainly maize crops)	Infected rodents with bubonic plague abundance	Tloma village, Kambi ya Nyoka village and Manyara region, Tanzania	McCauley et al. (2015)
Seed dispersal	Eurasian jay	Oak forest (National Urban Park)	Oak saplings abundance	National Urban Park of Stockholm, Sweden	Hougner et al. (2006)
	Flying fox	Tropical forest	Flying fox abundance, chewed diaspores	Vava'u Islands, Tonga	McConkey and Drake (2006)
	Thrushes	Temperate secondary forest	Seed abundance and richness and frugivorous abundance and richness	Cantabrian Range, Spain	García and Martínez (2012)
	Native frugivore birds	Tropical forest (Wild chillies)	Seedling emergence of gut passed seeds vs. non-gut passed seeds	Guam, Mariana Islands	Egerer et al. (2018)

butterflies and moths contribute to pollination of many crops, such as gourds, oilseeds, berries and tobacco, amongst many others (Roubik 1995, Williams 2002, Blanche and Cunningham 2005), as well as a countless number of wild plant species. Bees are probably the most recognised pollinators (>12,000 species; e.g. Kremen et al. 2002, Larsen et al. 2005, Morandin and Winston 2005, Potts et al. 2010, Kerr et al. 2015).

Biological control of pests and human diseases

Biological control is the natural process responsible for the regulation of species' population growth through ecological interactions –mutualism, parasitism and predation. This has been highlighted as a relevant regulation FES given the key role in restraining the spread of crop pests and diseases (Wilby and Thomas 2002, Fiedler et al. 2008, Karp and Daily 2014).

Oerke (2006) made an estimation of potential and actual losses due to pests for wheat, rice, maize, potatoes, soybeans and cotton, between 2001 and 2003, worldwide. Arthropod pests destroy 8–15% of these crops and without natural biological control and pesticides, this figure could reach 9–37%. According to the estimation done by Losey and Vaughan (2006), crop damage due to the absence of arthropod native predators might cost approximately US $4.5 billion more than the actual cost given pest control services.

Predation is one of the best-known mechanisms of biological control for agricultural pests and birds and bats have been identified as the main contributors, by their predation of species responsible for crop damage (Mols and Visser 2007, Maas et al. 2013, Karp and Daily 2014, Railsback and Johnson 2014). Increasing knowledge of the relevance of predators for pest control has increased the concern to conserve the conditions required to maintain these predators (e.g. Williams-Guillén and Perfecto 2010, Railsback and Johnson 2014).

Parasitoidism is considered another important mechanism of agricultural pest control (Drechsler and Settele 2001, Letourneau et al. 2015). The main providers identified are flies and parasitoid wasps, which lay eggs on or in the body of a host, in this case pest insects, eventually killing the hosts and diminishing the spreading of the pest.

Mutualism has been identified as another mechanism that can contribute to pest control. Perfecto and Vandermeer (2006) provided evidence that the mutualistic relationship between the Aztec ant and a coccid has a positive effect on coffee plants by reducing the numbers of the coffee borer beetle, coffee's main pest. This exemplifies the complexity of biological control mechanisms and how an imbalance in ecological condition can negatively impact this FES.

Disease control is also recognised as a relevant FES (Ostfeld and LoGiudice 2003, Foley et al. 2005, McCauley et al. 2015). Wild and domestic animals are vectors for a wide range of infectious diseases that are potentially transmitted to humans (see Molyneux et al. 2008, Civitello et al. 2015). Healthy populations of animals (i.e. populations with the minimum number of sexually mature individuals required to secure their viability) and high diversity provide less risk of human infection, since the probabilities of vectors (e.g. flies and ticks) targeting humans as hosts decreases with higher availability of other host species (Keesing et al. 2006, Civitello et al. 2015). Disease control is a FES directly related to human health and well-being.

Seed dispersal

Animals are also relevant actors in seed dispersal. They drive plant gene flow, population dynamics and spatial structure in undisturbed habitats and contribute to regeneration of deforested habitats, by moving seeds from one site to another (Russo et al. 2006, García and Martínez 2012). Animals are considered long-distance vectors; they contribute to seed dispersal mainly by defecation and epizoochory (seeds adhere to the outside of animal bodies). These include ants, frugivorous terrestrial, arboreal and flying mammals and frugivorous and/or caching birds (Greene and Calogeropoulos 2002). Animal seed dispersal is an essential mechanism in the maintenance of temperate and tropical ecosystems (García and Martínez 2012) and are particularly important for large-seeded plants (Greene and Calogeropoulos 2002, McConkey and Drake 2006, Wenny et al. 2016). Approximately one-half of seed plant species are dispersed by animals (Wenny et al. 2016, Egerer et al. 2018).

The ecological value of faunal dispersal is well known (Russo et al. 2006, Wenny et al. 2016). However, in comparison with animal pollination and pest control, the quantitative assessment of the seed dispersal service by fauna is scarce. Seed dispersal benefits are spatially and temporally distant from the mother plant, making them difficult to measure, especially for tree species and species not used directly by humans (Wenny et al. 2016) and further quantitative assessment is required for this FES.

The economic value of animals for seed dispersal is even less well known than their ecological value (Wenny et al. 2016). Some studies have indirectly estimated the value of animal seed dispersal through the economic valuation of associated food and fibre consumed by humans (e.g. Fujita and Tuttle 1991, Paoli et al. 2001). However, studies on direct valuation are scarce. A direct economic valuation is made by Hougner et al. (2006), who value seed dispersal carried out by the Eurasian Jay in an oak forest, through the estimation of the cost of replacing birds by human force.

Some of the studies where the role of animals in seed dispersal has been assessed are in tropical ecosystems. McConkey and Drake (2006) highlighted the relevance of flying foxes to sustain Pacific island forests, since these are the only existing animals capable of dispersing large seeds over long distances in such isolated habitats. Egerer et al. (2018) showed that bird dispersal provides a benefit to wild chilli plants in Guam through increased seedling emergence of gut-passed seeds in comparison to depulped seeds and whole fruits.

The role of richness and abundance of regulation faunal ecosystem service providers

Species richness (i.e. the number species present in a certain area) is considered the most simple and direct measure of biodiversity (Gotelli and Colwell 2001) and has been considered an important trait to evaluate the ecosystem services-biodiversity relationship (e.g. Egoh et al. 2009, Schneiders et al. 2012). There is the assumption that high species richness has a strong positive relationship with ES production and by conserving biodiversity, ES can be secured and improved (de Groot et al. 2010, Cardinale et al. 2011, Cimon-Morin et al. 2013, Isbell et al. 2015). However, this idea has been widely debated (Schwartz et al. 2000, Ridder 2008, Kleijn et al. 2015).

An empirical literature review by Schwartz et al. (2000) found little support for the hypothesis that there is a strong dependence of ecosystem function on species richness. They describe a curvilinear response where ecosystem function reaches saturation at low levels of species richness, indicating that few species can be enough to fulfil ecosystem functions. Equally, Ridder (2008) pointed out that most ES are not provided by all the extant species in a given ecosystem, but by any group of species that meet certain basic functional criteria or by species that are dominant and especially resilient in the face of change. In this sense, they highlight that using this argument could be counterproductive for both biodiversity and multiple ES conservation, since it would focus only on the conservation of a few "functional" species.

In contrast, Hector and Bagchi (2007) concluded that large numbers of species are necessary to fulfil the inherent multi-functionality of ecosystems. As more ecosystem functions were included in their analysis, more species were found to affect the overall functioning. Isbell et al. (2011) argued that species may appear functionally redundant when only one function is considered under one set of environmental conditions, but many species are needed to maintain multiple functions at multiple times and places. Bastian (2013) argued that species are embedded in an ecosystem and the loss of a single species (or population) and/or ecosystem function might have unpredictable effects. Therefore, conservation of all ES does imply conservation of biodiversity, even though many services are unrelated to species diversity or abundance and more related to climatic and structural properties of vegetation and landscape as well as human demand for them (Mulligan 2018).

Regarding regulation FES, there is evidence that, by increasing species richness, FES provision is improved. For instance, Larsen et al. (2005) showed how a decrease in bee species diversity considerably disrupts the pollination service. The meta-analysis carried out by Civitello et al. (2015), provided evidence that host diversity inhibits wildlife and human parasite abundance. Concerning seed dispersal, García and Martínez (2012) described a positive relationship between frugivorous birds richness and all the indicators of dispersion evaluated.

Abundance (i.e. number of individuals per species), rather than species richness, has been suggested as the most important trait that influence FES occurrence (Harrison et al. 2014, Winfree et al. 2015), particularly for pest regulation and pollination. According to the analysis carried out by Winfree et al. (2015), abundance of the dominant species is the main driver of ES delivery, while rare species are important for species richness but have little contribution to ecosystem functioning.

Some studies have evidenced the relevance of abundance of beetles (Blanche and Cunningham 2005), midges (Frimpong et al. 2011) and bees (Morandin and Winston 2005,2006) for crop pollination. Equally, predator abundance appears to be a determinant for the pest control service (Koh 2008, Crowder et al. 2010, Maas et al. 2013). The evidence above suggests that, unlike for many other classes of ecosystem service, animal species richness and abundance is required to secure regulation FES provision.

Faunal ecosystem disservices

Ecosystem disservices were recently defined as the ecosystem generated functions, processes and attributes that result in perceived or actual negative impacts on human well-being (Shackleton et al. 2016). Although there is literature addressing ecosystem disservices across several scientific disciplines, such as natural disaster management, agriculture and public health (Lyytimäki and Sipilä 2009, von Döhren and Haase 2015, Shackleton et al. 2016), the concept and theoretical framework around it are relatively new and undeveloped compared to that of ecosystem services (Shackleton et al. 2016) and associated literature is scarce (von Döhren and Haase 2015).

For many years, the assessment of the links between ecosystems and human well-being has been focused only on ecosystem services (Lyytimäki and Sipilä 2009). However, there are strong links between services and disservices: the same ecosystem function or component can be a source of service or disservice simultaneously (Zhang et al. 2007, Limburg et al. 2010, Escobedo et al. 2011; Figure 1).

The designation as service or disservice depends on the perceived influence on human well-being (Lyytimäki and Sipilä 2009). For example, a pollinator insect population can act as service provider by pollinating native plants and act as disservice provider by pollinating invasive plants in the same ecosystem. Therefore, to enhance our understanding of the ecosystem-human well-being relationship, we should aim for an integrative examination of ecosystem services and disservices (Ninan and Inoue 2013, Shackleton et al. 2016).

An integrative and balanced approach to services and disservices provides a better foundation for environmental management and conservation efforts (Lyytimäki 2015). With this aim in mind, Shackleton et al. (2016) proposed a working definition, characterisation and first categorisation for ecosystem disservices. They recognise that manifestation of disservices can be direct, i.e. impacting directly on human well-being (e.g. crop raiding by medium or large sized mammals) or indirect, by diminishing the flow or causing the loss or impairment of ecosystem services (e.g. invasive species altering native pollinator-plant relationships). Regarding categorisation, they consider two main aspects: origin of the disservice as biotic or abiotic and nature of the impact, as economic, health (health and safety) and cultural (aesthetic and cultural). According to this typology, the disservices related to agriculturalisation here termed faunal ecosystem disservices, belong to Shackleton et al's (2016) bio-economic and bio-health categories (Table 2). The disservices addressed here are: impacts of invasive species, spread of human diseases, crop pests and crop raiding.

Invasive species

Effects of invasive species on native species are well documented (e.g. D'Antonio et al. 2004, Alpert 2006) and, more recently, their effects on ecosystem services has also drawn attention (Pejchar and Mooney 2009, Pyšek and Richardson 2010, Peh et al. 2015, Walsh et al. 2016). According to Pejchar and Mooney (2009), the impact of alien species is usually well quantified for provisioning services (food, fibre and fuel). However, impacts on regulation FES are rarely calculated, but are likely to be substantial.

Amongst the reported effects of invasive species on animal pollination services are: the disruption of mutualism between native bees and plants by invasive bees, the range expansion in pollinator-limited invasive plants and consequent distraction of pollinators from native plant species (Stokes et al. 2006, Traveset and Richardson 2006). According to the review made by Morales et al. (2017), the impacts of invasive pollinators on pollination are predominantly negative for native plants, mixed for crops and positive for invasive plants. Although invasive pollinators can be beneficial for some native plants in highly disturbed habitats and some crops in intensively modified agroecosystems (e.g. Ricketts et al. 2004), they cannot replace the role of a diverse pollinator assemblage for wild plant reproduction and crop yield.

Table 2. Faunal ecosystem disservices. Selected examples of disservices related to agriculturalisation caused by fauna, describing providers, type of manifestation: direct or indirect (when causes decrease or loss of a service), category (according to Shackleton et al. 2016) and impact on human well-being.

Provider	Manifestation	Category	Disservice	Reference
Invasive pollinators	Indirect (pollination)	Bio-economic	Disruption of native pollinator-plant relationship, spreading of invasive plants	Traveset and Richardson (2006), Morales et al. (2017)
Herbivore insects	Direct (herbivory)	Bio-economic	Damage to crops	Pimentel et al. (2005)
Birds and mammals	Direct (crop riding)	Bio-economic	Damage to crops	Naughton-Treves and Treves (2005), Ango et al. (2016)
Invasive hosts	Indirect (disease control)	Bio-health	Novel hosts increase incidence of diseases, decrease of vertebrate population increases the risk of transmission to humans	Pejchar and Mooney (2009), McCauley et al. (2015)
Invasive frugivores and herbivores	Indirect (seed dispersal)	Bio-economic	Disruption of native seed disperser-plant relationship, spreading of invasive plants, emergence of new ecological associations	Richardson et al. (2000), Gosper et al. (2005)

Invasive species like weeds, insects and plant pathogens (mainly fungi) can become pests and have major impacts on crops. For instance, a well-documented case is the Mediterranean fruit fly, native from West Africa, but now found worldwide, which causes damage to over 250 types of crops. The cost estimated for California reaches US $1 billion (Mooney 2005). Similarly, Pimentel et al. (2005) made a detailed review of the environmental and economic costs associated with alien species in the United States. Related to crops, pasture and forest losses, they identify 500 weed species, feral pigs, European starlings, over 900 insect species and 20 plant pathogen species, as the main agents. The cost of losses, damages and control techniques reaches an annual value of approximately US $50,000 million.

Animal seed dispersal can be a disservice when this involves the spread of invasive plants. Just like the service, the knowledge on how animals contribute to the success of invasive plants is limited (Gosper et al. 2005). However, several mechanisms have been identified: the invasive plant species rely on common native disperser species with generalist diets; the invasive plant is reunited with the disperser species of its native range — like the case of *Rubus* spp. and blackbirds (*Turdus merula*) in Australia; and a new association between plant and animal can occur — like the case of the accidental spread of seeds of wind dispersed pines, *Pinus* spp., by seed predating cockatoos, *Calyptorhynchus* spp., in Australia (Richardson et al. 2000). Additionally, the dispersal of native plants is affected by the competition of dispersal service from invasive plant species (Gosper et al. 2005).

Equally relevant is the effect of invasive species on disease control: invasive plants and animals can act as novel hosts for diseases. Pyšek and Richardson (2010) provided detailed examples of how several invasive species affect human health, acting as vectors (e.g. rodents and bats as vectors of rabies, leptospirosis and hepatitis) or acting directly (e.g. snake bites).

Spread of human diseases

Overpopulation of disease organisms or disease vector organisms and/or the absence of defence organisms can increase the risk of spread for human disease. Many cases of disease outbreaks in human history have been related with invasive pathogens, due to the continual expansion and interchange of human population worldwide (Dobson and Carper 1996, Pejchar and Mooney 2009). For instance, the introduction of smallpox, measles and typhus with European arrivals to the New World increased mortality of the native human population at unprecedented rates (Dobson and Carper 1996). More recently, the increase of mosquito-borne diseases, like yellow fever and dengue, has been attributed to invasive mosquitoes in America and Asia (Pejchar and Mooney 2009). The negative effect can also be indirect, for example, the invasion of the American plant *Lantana camara* in East Africa. *L. camara* is now the habitat of the tsetse fly, vector of sleeping sickness.

Native species may also represent a risk for human health if the natural control of population growth is altered or if human contact with vectors increases. For instance, Ostfeld and LoGiudice (2003) evidenced how the risk of human exposure to Lyme disease increases due to the decrease in diversity of other hosts for ticks (Lyme disease vectors). Equally, McCauley et al. (2015) showed how changes in rodent and flea community composition due to LUCC, increase the abundance of *Mastomys natalensis*, transmitter of plague, in agricultural habitats in Tanzania.

Crop pests

Since the beginning of agriculture, humans have faced crop pests (Oerke 2006), which have had major impacts in human history. Pests, such as rusts on wheat, ergot on rye potato blight, gypsy moth and the boll weevil, have had deep social and economic consequences (Horsfall 1983). Currently 10–16% of global crop production is lost due to pests (Bebber et al. 2013).

Amongst the known causes of occurrence of crop pests is the imbalance of natural biological control, produced by a change in the abundance of natural enemy populations. For instance, a decrease in predator populations allows the increase of prey population (e.g. Drechsler and Settele 2001, Wilby and Thomas 2002, Karp and Daily 2014). Other causes are the absence of indigenous populations which facilitates the success of invasive species with similar ecological requirements (Pejchar and Mooney 2009) and the concentration of food resources, especially in perennial monocultures (Risch 1981, Altieri 2018). Although crop pests have been present since the appearance of agriculture, modern agricultural practices, like agricultural intensification (e.g. Wilby and Thomas 2002), manipulation of soil fertility and irrigation (e.g. Fuller et al. 2012) and use of chemical pesticides (Rosenzweig et al. 2001) have exacerbated these causes (Tilman 1999).

Crop raiding

Crop raiding is the term used to describe the action of wild animals foraging or trampling crops (Hill 2016). In this context, wildlife is considered a pest. However, this is not produced by an imbalance in wildlife populations, but by the increasing overlap of human and wildlife niches, due to continuous human population growth and the anthropogenic transformation of habitat (Hill 1997, Campbell et al. 2000). The most commonly identified actors are medium and large sized mammals (e.g. monkeys, wild pigs, hippopotamus, elephants; Naughton-Treves 1998, Engeman et al. 2010, Ango et al. 2016), but some studies also refer to small mammals and birds (e.g. Naughton-Treves and Treves 2005). Amongst the identified factors influencing crop raiding are the distance from cropland to natural habitat patches, the crop type and hunting practices (Naughton-Treves 1998). Drought, leading to paucity of production in (non-irrigated) natural lands, can also act as a push factor alongside the pull factor of higher productivity in irrigated or improved agricultural areas (Mulligan 2018).

Literature on this subject is extensive and mostly consists of case studies. The approaches to quantify losses vary considerably and are not comparable from site to site (McGuinness and Taylor 2014). The impacts have been assessed in human settlements adjacent to natural protected areas, where the raiding occurs frequently (e.g. Sekhar 2002, Linkie et al. 2007, Hedges and Gunaryadi 2010). However, there are also studies that address this phenomenon outside of protected areas (e.g. Ango et al. 2016, Chaves and Bicca-Marques 2017).

The extent of damage varies widely depending on where the raiding occurs and the type of crops and wildlife species involved. For instance, the socioeconomic impact might be higher in developing countries in non-protected areas with farmers losing their livelihood and rarely being compensated for the losses, thereby creating antagonism towards wildlife (Linkie et al. 2007). In contrast, in protected areas, prevention and compensation measures are more frequently enforced (Sekhar 2002, Davies et al. 2011).

The approaches to estimate monetary losses are variable, varying in unit of measurement and spatial scale. For example, Chakravarthy and Thyagaraj (2005) estimated a loss of US $8 per kilogram of dry capsules of cardamom caused by the Bonnet macaque (*Macaca radiate*), while Engeman et al. (2010) estimated that Rhesus macaque (*Macaca mulatta*) and Patas monkey (*Erythrocebus patas*), both invasive species, causes a nationwide economic impact of US $1.46 million per year in Puerto Rico.

Human-driven environmental changes strongly influence the occurrence of faunal disservices. Simultaneously, these environmental changes have an adverse effect on faunal services through the negative impact on the providers, mainly caused by the loss or transformation of habitat.

Effect of agriculturalisation on regulation faunal ecosystem service providers

Agriculturalisation is considered to be the main driver of loss, modification and fragmentation of habitats, causing biodiversity loss and ES degradation globally (Gaston et al. 2003, MA 2005). Ramankutty and Foley (1999) estimated that nearly 10.7 million km^2 of forests/woodlands and savannahs/grasslands have been transformed to agricultural land globally between 1700 and 1990. Temperate regions of developed countries experienced the greatest changes during nineteenth century, whilst most tropical developing countries have faced the greatest change from the late twentieth century to the present (Goldewijk 2001). In the past, the change conversion was mostly natural grasslands, whilst currently forests are the agricultural frontier. During the period from 1990 to 2015, there was a net loss of 129 million ha of forests worldwide (FAO 2015). Tropical forests present the highest rates of LUCC (anual rate 0.13%; FAO 2015), mainly for industrial export agriculture, traditional shifting agriculture and cattle ranching (Grau and Aide 2008).

Landscape homogenisation and habitat fragmentation

Landscape heterogeneity refers to the variety of different landscape conditions within a landscape (i.e. area that is spatially heterogeneous in at least one factor of interest, Turner and Gardner 2015) as with mixed habitats or land cover types. A closely related concept is landscape complexity, which can be defined as the level of difficulty observed in understanding the interactions of the landscape components (Papadimitriou 2010). The relationship between these concepts is controversial. Heterogeneity has been described as a function of complexity (e.g. Chen and Xu 2015), at the same time, heterogeneity has been considered an attribute of complexity (e.g. Papadimitriou 2010); furthermore, the terms have been used interchangeably (e.g. Miles et al. 2012).

The inconsistency in the use of terms makes the comparison and synthesis of studies difficult (Reyes Sandoval 2017). However, for practical purposes, we consider that loss of complexity/heterogeneity or landscape homogenisation/simplification refers to the same phenomenon: loss of components and/or loss of the interaction amongst components in a landscape.

The idea that the diversity of landscape components is a key determinant for biodiversity is widely accepted (Fahrig et al. 2011, Katayama et al. 2014). Increased landscape heterogeneity is generally associated with increased biodiversity, since high habitat and resource diversity allows high diversity of species, while the opposite, i.e. landscape homogeneity, is associated with low biodiversity (Parks and Mulligan 2010, Stein et al. 2014).

A consequence of LUCC due to agriculture is landscape homogeneity, as different land cover and habitat types are converted to more uniform agricultural land. Therefore, the proportion of agricultural land is the most commonly used indicator of homogenisation in studies where the relationship between biodiversity and landscape heterogeneity is assessed (e.g. Letourneau et al. 2015, Maas et al. 2016, Jonason et al. 2017). Other indicators include distance from original habitat (e.g. Blanche and Cunningham 2005, Ricketts et al. 2008) and diversity and management indices (Gardiner et al. 2009, Williams-Guillén and Perfecto 2010, Chaplin-Kramer et al. 2011).

Several studies support a positive relationship amongst landscape heterogeneity, species diversity and abundance of FES providers (Table 3). Although neutral or mixed relationships have also been evidenced (Jonsen and Fahrig 1997, Chaplin-Kramer et al. 2011), due mostly to species' particular ecological traits and range sizes (Katayama et al. 2014), landscape heterogeneity has proven to be a relevant factor in ecosystem functioning and population dynamics. Sustainable landscape management is suggested as the most important means of maintaining healthy populations of FES providers (Ricketts et al. 2008, Maas et al. 2013, Letourneau et al. 2015). There is also evidence that homogenised landscapes favour the occurrence of disservices by reducing the diversity and abundance of beneficial arthropods, such as pollinators and parsitoid insects and vertebrate predators (e.g. Letourneau et al. 2015, Senapathi et al. 2015, Maas et al. 2016) and thus increasing the outbreaks of herbivore and diseases pests (e.g. Altieri 1999, McCauley et al. 2015).

Along with landscape homogenisation, agricultural intensification has led to original habitat loss and concurrently to habitat fragmentation. Habitat fragmentation refers to the reduction of continuous tracts of habitat to smaller, spatially distinct remnant patches (Wilson et al. 2016). Fragmentation alters habitat connectivity and quality, affecting biodiversity and ecosystem functioning negatively (Haddad et al. 2015). Equally, reduction of the original habitat of animal populations has increased the conflict between humans and wildlife and the risk of disease transmission (Campbell et al. 2000, Xavier et al. 2012).

The degradation of ecosystems by landscape homogenisation, habitat loss and fragmentation results in decreased carrying capacity to sustain all the organisms that inhabit these ecosystems, leading to continued population losses. The loss of populations precedes species extinction and, therefore, the reduction of biodiversity (Ceballos and Ehrlich 2002).

Several studies have suggested that the loss of genetically distinct populations globally is both absolutely and proportionally several times greater than the rate of extinction of species (Hughes et al. 1997, Ceballos and Ehrlich 2002, Gaston et al. 2003). Genetic variation amongst and within populations confers resilience to environmental change whereas the loss of individuals or populations increases the vulnerability of species, destabilises ecosystem functions and affects ES provision (Luck et al. 2003).

Population losses through habitat loss

Habitat loss and fragmentation are the main causes of population decline (Fahrig 1997, He and Hubbell 2011, Wilson et al. 2016). Hughes et al. (1997) estimate the population diversity, defined as the number of populations on the planet, for 82 species (35 vertebrates, 23 plants, 19 arthropods, four molluscs and one platyhelminth) in the range 1.1–6.6 billion populations. By using the midrange estimation (3 billion populations), assuming a linear function between population and habitat loss and that two-thirds of all populations exist in tropical regions, they estimate that 16 million populations are lost annually across these 82 species alone.

Table 3. Faunal ecosystem service providers and landscape heterogeneity. Examples of studies evaluating the relationship of landscape heterogeneity and FES providers richness and abundance, including the definition of heterogeneity as described by the studies' authors.

Group	Study type	Description of landscape heterogeneity	Relationship	Reference
Native bees	Original	Watermelon farms with gradient of agricultural intensification, 1% to ≥30% natural habitat within a 1-km radius	Positive	Kremen et al. 2002
Nitidulid and Staphylinid beetles	Original	Atemoya orchards with gradient of decreasing distance (0.1–24 km) from tropical rain forest	Positive	Blanche and Cunningham 2005
Bees, bumblebees and beetles	Meta-analysis	Isolation of several crops from natural habitats	Positive	Ricketts et al. 2008
Coccinellid beetles	Original	Soybean and corn crops with gradient of agriculturally dominated to forest and grassland dominated within a 3.5-km radius, landscape diversity measured as Simpson's D	Positive	Gardiner et al. 2009
Pollen beetles, stem weevils	Original	Various crops with gradient ranging from structurally poor to complex landscape at several spatial scales (250–2000 m radius), landscape diversity measured with Shannon-Wiener index	Mixed (Scale-dependent)	Zaller et al. 2008
Leaf-Nosed Bats	Original	Coffee plantations and forest fragments along a gradient of management intensity, landscape diversity measured with Management Index	Mixed (Trophic guild-dependent)	Williams-Guillén and Perfecto (2010)
Natural enemies of pests	Meta-analysis	Landscape complexity metric consider % natural habitat, % non-crop habitat, % crop, habitat diversity measured using Shannon and Simpson indices	Positive	Chaplin-Kramer et al. (2011)
Birds	Original	Coffee farms in sites of mixed cropland and habitat vs. separate areas of intensive agriculture and habitat	Positive	Railsback and Johnson (2014)
Parasitic wasps and flies	Original	Rotatory organic crop fields ranging from homogenous cover of annual crops to primarily forest trees and native shrubs within 500 m and 1500 m radius	Positive	Letourneau et al. (2015)
Bees and wasps	Original	Historical land cover change using spatial analysis within 1, 2, 5 and 10 km radii	Positive	Senapathi et al. (2015)
Birds and bats	Review	Cacao, coffee and mixed fruit orchards and tropical forest sites, comparison among forest, agroforestry and agricultural systems	Mixed (Taxa-dependent)	Maas et al. (2016)
Arthropods enemies of aphids	Meta-analysis	Proportion of cultivated land within a 1 km radius around each plot	Positive	Rusch et al. (2016)
Wild bees	Original	50 ha landscape plots in agricultural areas with increasing cover of semi-natural and natural vegetation patches	Positive	Bukovinszky et al. (2017)
Butterflies and farmland birds	Original	Proportion of arable field cover	Positive	Jonason et al. (2017)

Ceballos and Ehrlich (2002) made an indirect estimation of mammal population loss globally, by comparing present and historic ranges of 173 declining species, reaching a collective loss of 50% of range area. Regarding bird populations, Gaston et al. (2003) estimated a loss of approximately 22% of breeding bird individuals so that an average of 87 billion breeding bird individuals remain from approximately 112 billion estimated before 1700, which is considered the starting date for development of the current pattern of LUCC due to agriculture.

Global declines in pollinator populations are widely recognised (Biesmeijer et al. 2006, Gallai et al. 2009, Potts et al. 2010) and habitat loss is considered the main threat, particularly for habitat and plant specialists (Ricketts et al. 2008, Potts et al. 2010, Winfree et al. 2015). Equally, decline in predator and parasitoid populations due to habitat loss has been reported (Williams-Guillén and Perfecto 2010, Letourneau et al. 2015).

Population losses through microclimatic changes and edge effects

LUCC causes microclimatic changes in the remaining patches of ecosystem related to temperature, wind and humidity (Meyer and Turner 1992). There is evidence that deforestation can modify local rainfall and droughts pattern, changes in moisture and humidity can also negatively affect canopy, understorey and litter organisms and can increase fire frequency in tropical and arid ecosystems (Goldammer and Seibert 1990, Rao 2009), increasing the mortality of animal populations.

Along with climatic modification, physical changes diminish animal habitat suitability by reducing the quantity and quality of nesting, sheltering, and foraging sites (Frumhoff 1995). These changes can affect ecological interactions, survivorship, reproductive fitness and distribution of populations, particularly for highly specialised organisms (Dale 1994, Afrane et al. 2006, Rao 2009). Finally, the decrease in population sizes at the interface between two land cover types, known as the edge effect, is also enhanced by habitat fragmentation, caused by deforestation (Levin et al. 2009).

Population losses through pest proliferation and chemical pest control

Environmental changes caused by LUCC may adversely affect biological control processes. Spatial and temporal distribution and proliferation of insects, weeds and pathogens is largely determined by climate, therefore microclimatic changes in temperature, light and water supply can drive overpopulation of pests (Rosenzweig et al. 2001). Pest proliferation has detrimental consequences for ecosystems (Chapin et al. 2000, Wilby and Thomas 2002, Foley et al. 2005). For example, *Imperata cylindrica*, an aggressive indigenous grass, which colonises forest lands of Asia that are cleared for slash-and-burn agriculture, forms a monoculture grassland with no vascular plant diversity and few mammalian species in comparison with the native forest (Chapin et al. 2000).

Crop pests produce major losses for crop yields, therefore, farmers have resorted to the use of pesticides as a means of control. In the last six decades, there has been a dramatic increase in the use of pesticides. Along with agricultural intensification, herbicides, insecticides and fungicides have produced highly negative effects on species abundance and diversity (Geiger et al. 2010, Isenring 2010) and also threaten water quality (Vymazal and Březinová 2015) and human health directly (see Budzinski and Couderchet 2018) . There is evidence of the adverse effect of chemical pest control on farmland and wildlife populations worldwide (e.g. amphibians and reptiles, Gibbons et al. 2000, farmland birds, Boatman et al. 2004, benefitial arthropods, Desneux et al. 2007). Direct adverse effects include higher mortality due to poisoning, reduced fecundity and detrimental changes in physiology and behaviour. Indirect effects include reduction of habitat, due to destruction of non-invasive vegetation, reduction of food resources for predators by indiscriminate elimination of arthropod populations and imbalance in ecological interactions.

Impacts of biodiversity losses on provision of regulation faunal ecosystem services

It is sensible to assume that, by losing populations of providers, the production of ES might be compromised. However, it is crucial to understand the mechanisms that affect provision first. Several studies have evidenced the underlying reasons for the negative effect of population losses on FES production as outlined below.

Species richness loss

Regarding animal pollination, the high diversity in morphology and reproductive strategies of plants requires a similar diversity of pollinators (Blüthgen and Klein 2011). Therefore, a decrease in pollinator diversity potentially causes a decline in wild plant and crop diversity (Biesmeijer et al. 2006, Potts et al. 2010), as well as reduced crop productivity. Blanche and Cunningham (2005) observed a highly significant reduction in fruit set due to pollinator exclusion in atemoya crops. The risk is greater for wild or crop species that rely on a narrow range of pollinator species. Although the threshold of diversity, required to maintain pollination stability, depends on the biology and variety of crops, landscape structure and regional pollinator community, the evidence suggests that stability is higher with a diverse and abundant pollinator community (Klein et al. 2007).

Equally, a detrimental effect on natural pest control in crops has been identified due to a reduction in natural enemy diversity (e.g. rice crops, Drechsler and Settele 2001, Wilby and Thomas 2002, cacao plantations, Maas et al. 2013, coffee plantations, Karp and Daily 2014). Straub et al. (2008) indicated that higher diversity of predators implies higher complementarity on functional roles: feeding on different pest species, at different life stages of the pest, using diverse strategies and differential partitioning of space and/or time (e.g. eating pest insects from different parts of the plant or during different seasons). This explanation could also be applied to parasitoid species.

Human disease control can be affected by reduction in species richness. A 'dilution effect' (*sensu* Keesing et al. 2006), where increased species diversity reduces disease risk for individual species, has been described for some diseases (e.g. tick-borne diseases, Norman et al. 1999, Ostfeld and LoGiudice 2003, viral pulmonary disease, Ruedas et al. 2004, mosquito-borne diseases, Ezenwa et al. 2006, Allan et al. 2009). This indicates richness loss can lead to more disease. Keesing et al. (2006) provides a detailed explanation of the mechanisms through which higher species richness decreases disease risk, including: reducing the rate of encounter between susceptible and infectious individuals, reducing the probability of transmission given an encounter, decreasing the density of susceptible individuals, increasing the recovery rate and increasing the death rate of infected individuals.

Seed dispersal is also affected by diversity loss. García and Martínez (2012) found a clear positive relationship between richness of frugivorous birds and all components of seed dispersal (i.e. seed richness and abundance and arrival and colonisation rates). Just like pollination and biological control, this suggests the existence of functional complementarity and/or facilitation amongst dispersers.

In general, even though initial species loss can be compensated by remaining species with similar functions, significant species loss will eventually reduce provisioning of FES. Therefore, to secure FES production, it is essential to conserve species richness.

Population loss

Along with species richness, population size or abundance, are determining factors for FES provision. Since population losses are higher than diversity losses (Ceballos and Ehrlich 2002, Gaston et al. 2003), these can have major implications on the magnitude and quality of FES provision.

Losses in pollinator populations produce a negative impact in wild plant communities, affecting the integrity of natural vegetation (Williams 2002, Biesmeijer et al. 2006). Additionally, population declines reduce crop production (Kremen et al. 2002, Larsen et al. 2005, Klein et al. 2007), causing important economic losses (Losey and Vaughan 2006, Gallai et al. 2009) and jeopardising food sufficiency worldwide (Aizen et al. 2009).

Equally affected is the pest control service, where abundance of natural enemies, predators and parasitoid species, largely determines the abundance of species that can become pests (Drechsler and Settele 2001, Mols and Visser 2007, Railsback and Johnson 2014). Like pollinators, losses in natural enemy populations cause losses in natural and agricultural systems (Losey and Vaughan 2006, Oerke 2006).

Regarding the disease control service, population size of hosts has a complex effect on transmission dynamics. Through model-based analysis, Norman et al. (1999), and

Gilbert et al. (2001) suggested that intermediate abundances of non-viraemic hosts (i.e. where pathogens do not enter the bloodstream) allow persistence in viraemic hosts, whereas high or low abundances lead to vector fadeout. Keesing et al. (2006) provided an example of how variation of population sizes of two rodent species through time affects disease spread: when there is a high density of chipmunks, there is a reduction in tick burdens on white-footed mice (the most competent reservoir for the Lyme bacterium). Losses in populations can lead to unpredictable effects on spread of vector transmitted diseases.

Decline in frugivorous populations reduce availability and quality of seed dispersal services (McConkey and Drake 2006, Peres and Palacios 2007). McConkey and Drake (2006) demonstrated that there is a threshold in population size for service provision; this is when the functionality of dispersers is lost, even before the individuals become rare. Therefore, the losses in disperser populations should not be dramatic to have a great impact on the seed dispersal service.

Thus, a decrease in abundance of FES providers has a negative impact on FES provision. Even though the reduction is small, the consequences on FES production can be significant given the complex interactions amongst the providers and the ecosystem functioning. Population losses imply more immediate effects than the loss of richness.

Potential impacts of future land use and cover change on faunal ecosystem service provision

While the understanding of the effects of current LUCC on ES provision has increased (Nelson et al. 2010), few studies have assessed the potential effects in the future (Nelson and Daily 2010). One of these is the assessment made by Lawler et al. (2014). They used LUCC models to assess the effects on the provision of carbon storage, timber production, food production and wildlife habitat. They projected LUCC from 2001 to 2051 for the United States under two scenarios: 1) a large increase in croplands (28.2 million ha) due to a high crop demand, mirroring conditions starting in 2007; and 2) a loss of cropland (11.2 million ha) mirroring conditions in the 1990s. These scenarios result in large differences in land-use trajectories that generate increases in ES from increased yields (even with declines in cropland area) and >10% decreases in wildlife habitat.

Mulligan (2015a) assessed the effects of agriculturalisation in Brazil and Colombia on carbon storage and sequestration, water services, hazard mitigation and species richness and endemism. He projected LUCC forward to 2100, using historic rates of conversion with new areas of agricultural growth based on agricultural suitability, proximity to current deforestation fronts and current and likely new transport routes, under two scenarios: 1) change is excluded from occurring in current protected areas and 2) change occurs both within and outside of protected areas. In both scenarios, there is a decrease in services, although it is lower in the first scenario. Similarly, Mulligan (2015b) assessed the effects of the same scenarios on these same services pantropically from 2010 to 2050. Results suggest rapid agriculturalisation in the tropics implying considerable threats to the remaining natural capital and ES provision.

Regarding FES, Aizen et al. (2009) modelled the potential expansion of cropland and the resultant decline of pollinator populations. Based on annual data compiled for 45 years (1961–2006), they estimated a decrease of 8% in agricultural production due to loss of pollinator population. Crops with the least yield growth over the last five decades generally had the greatest expansion of cultivated area – including avocado, blueberry, cherry, plums and raspberry, which are highly pollinator-dependent. Therefore, they predict an increase in cultivated area, particularly in the developing world – mostly distributed in the tropics. Potential effects of future agriculturalisation on other FES remain to be evaluated.

Although there is still much to know about the future impacts of LUCC on FES provision, it seems possible to assess changes in supply in relation to agriculturalisation.

Expected demand for regulation faunal ecosystem services

ES demand is the sum of ecosystem goods and services currently consumed or used in a certain area over a given time of period (Burkhard et al. 2012). Therefore, to assess demand for ES – or FES – we need to know the factors determining their use in order to infer changes in demand as these factors change with agriculturalisation. For instance, the increasing demand for food, derived from population growth, the growing diversification of human diet, particularly in industrialised nations and globalisation in food trade have increased demand for many animal-pollinated crops. This is likely to continue in the future (Aizen et al. 2009).

World population is expected to reach 9 billion people by 2050 and would require raising overall food production by 70% (FAO 2009). Production in the developing countries would need to almost double. This implies significant increases in the production of several commodities, including crops (Alexandratos and Bruinsma 2012). Since agricultural land has a high demand for regulation ES and FES (Burkhard et al. 2012), such as pollination, natural pest control or nutrient regulation, an increase in demand for these services is expected.

Today, the developing world represents more than two thirds of global agricultural production and cultivated land and supports agriculture, which per unit of production, is 50% more pollinator-dependent than that of the developed world (Aizen et al. 2009). Along with the increase in food demand, the shortage in pollinator population might result in an increase in demand for agricultural land (Aizen et al. 2009), since per unit area crop yield may be reduced in the absence of pollinators (Morandin and Winston 2005, Aizen et al. 2009), causing, in turn, more extensive demand of FES provision.

Human induced changes might increase the demand for natural disease control. For instance, the development of irrigation systems is likely to increase the risk of contracting diseases such as dengue and malaria, by favouring the breeding of vectors, like flies and mosquitoes, in areas where they were absent or rare (Fuller et al. 2012). Irrigated cropland has expanded considerably since 1970 and is projected to increase a further 20% worldwide by 2030, reaching almost 2,500,000 km^2 (Turral et al. 2010). Therefore, an increase in vector-disease outbreaks may be expected, as vectors may disperse to newly irrigated areas (Fuller et al. 2012).

Global forest area is projected to continue to decrease over the next years, although at a lower rate compared with the beginning of the century, declining from 0.13% to 0.06% per year by 2030 (d'Annunzio et al. 2015). This projection of forest area is the net result of increase in some regions and decrease in others. Faunal seed dispersal is a service that might help to regenerate and shape the forest structure in these areas, by allowing the seed movement of animal-dependent tree species. However, in general, based on the past and current information, the projections suggest an increase in FES demand due to agricultural expansion at the same times as there is a reduction in FES supply.

Conclusions

Ecosystem functions deliver final benefits or goods through the provision of ecosystem services where there is demand for them. To achieve proper management, conservation and valuation of such functions or of regulation ecosystem services and FES, an accurate characterisation is essential and understanding the providers of these services is a significant part. Animal populations are key providers of regulation services and simultaneously can be source of disservices. To secure the service provided and minimise disservices, it is imperative to continue studying their role, to understand the potential implications of their loss and to use this evidence base to advise conservation and sustainable land use.

We identified two components of faunal diversity as influential to FES provision, richness and abundance. Richness brings functional diversity and complementarity, improving the range of FES provision, while a higher number of species improves the magnitude and spatial distribution of provision, since it is abundance that determines the occurrence of these services. Speciose systems with low species abundance may have low or null FES provision.

Animal species may also be a source of disservices to people. We identified invasive and native species pest outbreaks as the most common sources of disservice. Animal populations can be the main actors or can act as vectors of viral, bacterial or fungal pests. The evidence suggests that invasive species can be an indirect source of disservice when disrupting the service provision by native species, while native species may impact directly as crop pests, human disease vectors or crop raiders.

Several studies suggest that agriculturalisation has negative effects on FES providers due to landscape homogenisation, habitat loss and fragmentation, microclimatic changes and population imbalance, causing species and population losses. This increases the occurrence of disservices, impacting FES production through the decrease of functional complementarity — in the case of pollination, seed dispersal and pest control — or dilution effect — for human disease control and increasing crop and disease pest populations and wildlife-human conflict.

Few studies have addressed potential effects of LUCC on FES provision under different scenarios of agricultural change. LUCC models can be used to drive models for current and future FES provision. Such analyses are particularly important given the expected concomitant increase in demand for FES as land continues to be converted for agriculture.

The effects of land use change on FES providers have been assessed mostly at the local scale, using a range of approaches. To improve understanding of these effects at wider scales, it is desirable to develop a common approach to allow comparison and to identify land use configurations that maximise FES provision. For this, further research is required; first, to know the spatial distribution of FES providers; second, to identify the suitable conditions that allow FES providers to provide the FES and third, to relate these conditions to characteristics of land use and cover. Moreover, to date, the different FES have been evaluated independently: analysing them together can provide valuable information about distribution patterns, synergies and trade-offs amongst them.

Conservation prioritisation must factor in faunal ecosystem services (and disservices) as the most biodiversity-relevant of all ecosystem services and those which most closely links sites of conservation value that provide services with nearby sites of service use of agricultural and economic value. This will require the development of spatial models of faunal ecosystem services and disservices to compliment the ecosystem service models in existing tools such as Co$ting Nature (Mulligan et al. 2010, Mulligan 2015b) and InVEST (Tallis and Polasky 2009) and to drive these for baseline and scenarios of land use using LUCC models.

Maximum robustness of modelling results for policy formulation is achieved by using an ensemble of ecosystem service models, as has been common practice with climate models for decades. Each rigorous new approach to modelling faunal ecosystem services that is globally applicable and inter-operable or capable of comparison with existing models, can be a valuable contribution to improving our understanding of this important class of ecosystem services.

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2.3. Conclusion

This chapter summarised the evidence on the relationship between fauna and ES provision and the effects of agriculturalisation on it. This allowed the identification of key concepts, such as ES providers and faunal ecosystem services; key functions, like pollination, biological control and seed dispersal; the roles of richness and abundance in service provision; and some gaps in research, such as the development of multi-FES models at broader scales, and the use of LUCC models to assess future FES conditions of provision and demand. The opportunity to reduce these gaps is addressed in the following chapters.

3 A pantropical pollination model

3.1. Introduction

This chapter presents the work carried out to fulfil the second objective of this thesis, to generate a pantropical spatial distribution model of a FES provision and demand. Spatially explicit models of ES are valuable tools to understand the potential effects of LUCC and inform management decisions (Costanza et al. 2017).

The developed spatial model of pollination service was focused exclusively on wild bees. This model is based on two main features to estimate pollination provision: habitat suitability and mobility of providers (Lonsdorf et al. 2009, Zulian et al. 2013). The general structure and assumptions of this model are depicted in Fig. 3.1, the theory and methods used to generate it are described in Section 3.2. This section is presented in the format of a research article, which has been submitted for publication and is currently under review. This article aimed to answer the following questions:

a) Where is the pollination service provided by wild bees to cropland distributed in the tropics?
b) How much of this service is currently protected?
c) What tropical protected areas (PAs) contribute to service conservation?
d) What is the relationship between service distribution and size of PAs?

Based on the idea that habitat suitability and mobility determine the occurrence of pollination service, we tested the hypothesis that the highest service provision occurs in cropland located nearby PAs, where pollinators can access both suitable nesting sites and floral resources.

The article has supplementary information containing a sensitivity analysis and detailed information on methods, which are available in the appendices of this thesis.

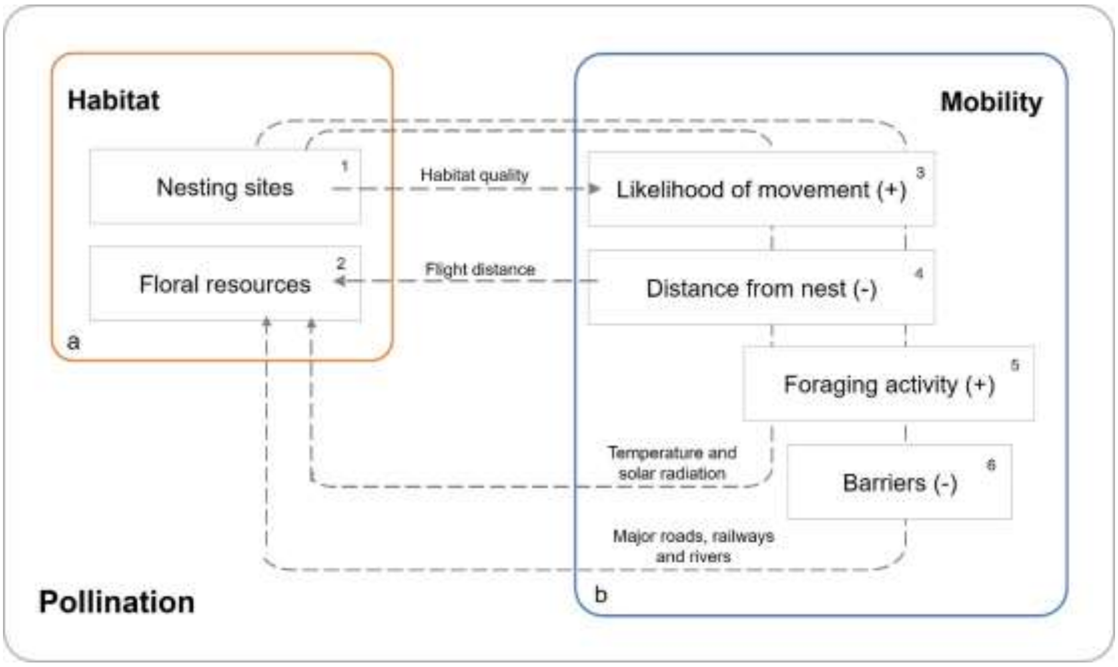


Figure 3.1. Pollination model. The proposed model was based on two main features, (a) habitat suitability and (b) mobility of pollinators, i.e. wild bees. Habitat suitability was defined as the availability of (1) nesting sites and (2) floral resources. For pollination to occur wild bees must have access to floral resources from their nests, this is subject to their mobility. The factors used to model wild bee mobility were (3) the likelihood of movement, influenced by the quality of the habitat surrounding nesting sites; (4) the distance between the nest and floral resources, determined by the pollinators' flight distance; (5) the foraging activity, subject to environment temperature and solar radiation; and (6) the occurrence of barriers, i.e. major roads, railways and rivers. These factors can have a positive (+) or a negative (-) effect on pollination service by wild bees.

3.2. Research article: Small-sized protected areas contribute more to tropical crop pollination than large protected areas

Pollination provided by animals is an essential process for the maintenance of wild plant communities and service for agricultural systems (Potts et al. 2010). Over 87% of flowering plant species are directly dependent on animal pollination globally (Klein et al. 2007, Ollerton 2017) and over 66% of the world's crop species depend on pollinators and produce between 15 and 30% of global food production (Kremen et al. 2002, Klein et al. 2007).

Approximately 70% of tropical crop production is supported by wild pollinators (Roubik, 1995). A species-rich and abundant community of pollinators with high species richness and abundance generally provides more effective and stable crop pollination (Klein et al. 2007, Potts et al. 2016). Insects are the most important pollinators in terms of abundance and foraging behaviour (Kremen et al. 2002), with bees the best-known group. The global decline in pollinating insect populations is widely recognized (Biesmeijer et al. 2006, Potts et al. 2010). Land use and cover change are considered some of the main threats at broader scales (Ricketts et al. 2008, Potts et al. 2016, Gutierrez-Arellano and Mulligan 2018).

Land conversion reduces the availability of nesting substrates and floral resources for wild pollinators, which are the most influential factors for pollinator diversity and abundance (Potts et al. 2005, Williams and Kremen 2007, Lonsdorf et al. 2009). Deforestation is an indicator of land use and cover change, and currently, the greatest forest loss occurs in the tropics (FAO 2015). Protected areas (PAs) in tropical forests have an important role in safeguarding nesting and foraging sites of wild pollinators, and consequently in conserving wild plant communities and yields in pollinator-dependent crops.

The relevance of the occurrence of natural habitat patches near cropland for pollination provision has been widely studied at the landscape scale, showing a positive relationship (e.g. Ricketts et al. 2008, Senapathi et al. 2015b, Bukovinszky et al. 2017). The value of PAs to provide and conserve this service has been recently assessed in the tropics at the local scale (Hipólito et al. 2019). Here, we assessed this on a pantropical scale.

The spatial configuration of PAs has been a topic of concern in conservation science for decades (Williams et al. 2005) and the effect of PA size on effectiveness for biodiversity protection has been widely debated (Ovaskainen 2002, Tjørve 2010). More recently, with the recognition of need and benefit of simultaneous protection of biodiversity and ecosystem services (Goldman et al. 2008, Watson et al. 2019), ecosystem services have been increasingly included in this debate (Eigenbrod et al. 2009, DeFries et al. 2010). The optimal spatial configuration for PAs varies depending on conservation outcomes (Maiorano et al. 2008), however, small-sized PAs have been identified as highly valuable for biodiversity and ecosystem service protection and particularly vulnerable to land-use change (Bodin et al. 2006, Maiorano et al. 2008, Eigenbrod et al. 2009, Wintle et al. 2019).

Most of the knowledge about the current status of diversity and abundance of wild pollinators, as well as the effects of land conversion on service provision at broad scales, is based on data from North America and Europe (Lonsdorf et al. 2009, Zulian et al. 2013), data for other regions is still insufficient (Potts et al. 2016). Modelling is especially useful in areas where measured data may be sparse such as tropical regions (Bullock and Ding 2018). A spatially explicit model of tropical wild pollinators can be a useful tool to inform land use and development decisions (Costanza et al. 2017).

Here, we developed a spatially explicit probabilistic model of pollination service to crops aimed for tropical regions. We built this model on the theoretical frameworks proposed by Lonsdorf et al. (2009) and Zulian et al. (2013) used to map pollination service in North America and Europe, respectively. They suggest nesting suitability of land cover type, availability of floral resources and bee mobility as the most relevant factors to estimate wild pollinator abundance. While we considered these factors, we also suggest key modifications to bee mobility variables. Although other non-bee insects, including flies, beetles, moths, butterflies, wasps, ants, and some birds, and bats, are important contributors to crop pollination (Rader et al. 2016), this model focuses only on bee pollinators, all assumptions are based entirely on bee species.

The objective of this study was to estimate how much of the pollination provided by wild bees is currently found within tropical protected areas, as an indicator of protection of the service, and how much can contribute to the pollination of tropical crops. Based on this we made an initial assessment of the role of PAs size in service provision. We identified which protected areas contribute most to the provision of pollination service to crops and identify some key patterns and their implications for management.

3.2.1. Methods

3.2.1.1. Study area

The study area includes all the terrestrial PAs within the tropical forest area. Tropical forest area delimitation was based on the terrestrial ecoregions map (NC 2012), these include tropical and subtropical coniferous forests, tropical and subtropical dry broadleaf forests and tropical and subtropical moist broadleaf forests. Data on PAs was obtained from the World Database of Protected Areas (IUCN and UNEP-WCMC 2017). The extent of the analysis was restricted between 35.0 and -35.0 degrees of latitude, where the tropical and subtropical forest distribution is delimited.

3.2.1.2. Pollination model

Evidence suggests that pollinator species richness (Garibaldi et al. 2011, Mallinger and Gratton 2015, Dainese et al. 2019) and abundance (Harrison et al. 2014, Winfree et al. 2015) are necessary components of pollinator diversity to sustain and magnify pollination service. Species richness is relevant for specialist interactions and pollination effectiveness (Dainese et al. 2019, Guzman et al. 2019), while the abundance of pollinators enhances pollination services (Blanche and Cunningham 2005, Morandin and Winston 2006, Frimpong et al. 2011). The model we propose focuses on the estimation of wild bee abundance.

The proposed model combines a probability of occurrence of wild bees −based on the occurrence of suitable habitat, i.e. nesting sites and floral resources− and their probability of movement and activity to provide a relative index of potential service provision per cell (cell size 300 m), ranging from 0 (null capacity of provision) to 1 (maximum capacity of provision). This potential pollination model is linked with the current distribution of pollinator-dependent crops to generate a realised pollination model. The difference between these models is that potential pollination depicts where the service is provided but not necessarily consumed (now or in the future), and realised pollination shows where the service is currently consumed, i.e. pollination of tropical crops. This probabilistic approach to model pollination aims to capture the variation in the occurrence of this process (code available here and a sensitivity analysis is described in Appendix A).

Potential pollination

Using geographic information system techniques (Fig. 3.2), open-source global spatial data and literature, we generate the following variables to model potential pollination:

1) *Nesting suitability by land cover type*. The GlobCover 2009 land cover map (Arino et al. 2010) was the base map used to assign suitability scores for nesting (N_j) throughout the study area. These values range from 0, land cover is unsuitable for nesting, to 1, land cover provides suitable sites for nesting in full extent (i.e. 100% of the pixel provides optimal nesting conditions; e.g. water bodies, 0; artificial or urban areas, 0.3; mosaic forest-grassland 0.9; Table 3.1). The assignment of these values is based on the values suggested by Tallis et al. (2011) and Zulian et al. (2013). These are based on literature and expert assessment.

2) *Corridors*. Marginal habitats such as roadsides and stream banks in semi-natural zones have a positive impact on nesting suitability and floral availability in highly-modified landscapes (Svensson et al., 2000; Zulian et al., 2013). These may supply diverse nesting opportunities and higher floral diversity in comparison with the surrounding ploughed fields (Hopwood, 2008; Kwaiser and Hendrix, 2008). Therefore, the nesting suitability and floral availability scores for those cells with a modified landscape and containing rivers (FAO 2014b), railways (FAO 1997a) and/or roads (FAO 1997b) were modified to a value of 0.8 (Zulian et al. 2013) for marginal habitats in modified landscapes (i.e. Post-flooding or irrigated croplands, rainfed croplands, mosaic cropland, mosaic vegetation). These constituted an additional land cover type to those originally proposed on the GlobCover 2009 map.

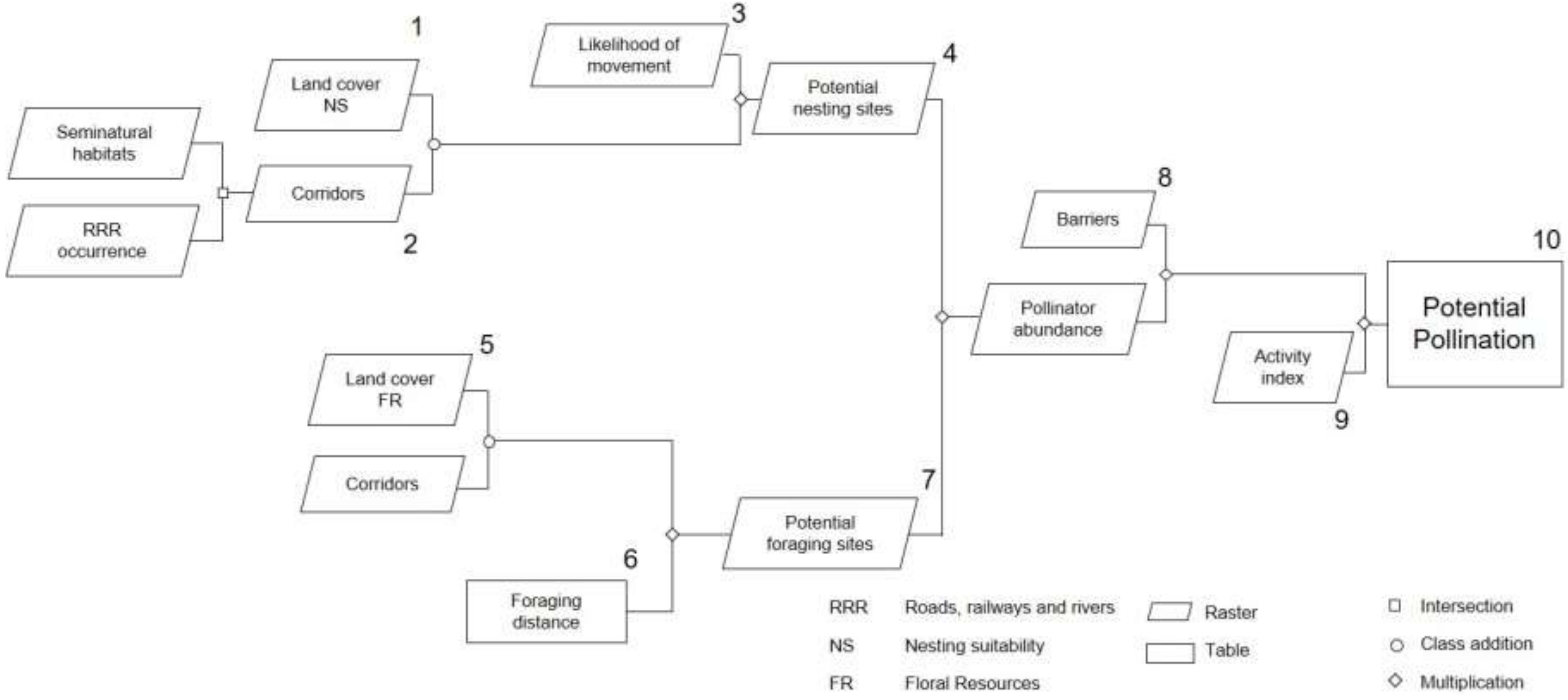


Figure 3.2. Potential pollination model workflow. Flow chart describing the spatial (raster data) and non-spatial data (table) used to derive the final potential pollination map, using map algebra. Numbers indicate the description of each variable in the main text. Abbreviations: RRR= roads, railways and rivers; NS= Nesting suitability; FR= Floral resources. Grey text in dotted boxes represents intermediate rasters.

Table 3.1. Suitability of nesting and foraging sites by land cover type. Scores of GlobCover 2009 land cover classes according to nesting suitability (NS) and floral resources (FR) for tropical bees, as suggested by the models of Lonsdorf *et al.* (2009) and Zulian *et al.* (2013) and their equivalent land cover type descriptions. (*) Additional land cover class created ad hoc for this pollination model. The scores range from 0, absence of suitable sites or floral resources, to 1, the land cover provides suitable sites or floral resources in full extent.

GlobCover 2009 land cover types	**Lonsdorf *et al.* (2009) /Zulian *et al.* (2013) land cover types**	**NS**	**FR**
Post-flooding or irrigated croplands (or aquatic)	Irrigated perennial	0.4	0.4
Rainfed croplands	Non-irrigated arable land	0.2	0.2
Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)	Land principally occupied by agriculture, with significant areas of natural vegetation	0.7	0.75
Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	Land principally occupied by agriculture, with significant areas of natural vegetation	0.75	0.7
Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)	Broad-leaved forest	0.8	0.9
Closed (>40%) broadleaved deciduous forest (>5m)	Broad-leaved forest	0.8	0.9
Open (15-40%) broadleaved deciduous forest/woodland (>5m)	Broad-leaved forest	0.4	0.45
Closed (>40%) needle-leaved evergreen forest (>5m)	Coniferous forest	0.8	0.3
Open (15-40%) needle leaved deciduous or evergreen forest (>5m)	Coniferous forest	0.4	0.15
Closed to open (>15%) mixed broadleaved and needle-leaved forest (>5m)	Mixed forest	0.8	0.6
Mosaic forest or shrubland (50-70%) / grassland (20-50%)	Natural grassland/ Transitional woodland-shrub	0.9	0.9
Mosaic grassland (50-70%) / forest or shrubland (20-50%)	Natural grassland/ Transitional woodland-shrub	0.9	0.9
Closed to open (>15%) (broadleaved or needle-leaved, evergreen or deciduous) shrubland (<5m)	Moors and heathland	0.9	1
Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	Pasture/Grass	0.4	0.4
Sparse (<15%) vegetation	Sparsely vegetated areas	0.7	0.35
Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water	Flooded/marsh	0	0
Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water	Flooded/marsh	0	0
Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water	Flooded/marsh	0	0
*****Land cover types modified by agriculture and occurrence of roads, railways or rivers	Marginal habitats in modified landscapes	0.8	0.8

3) *Likelihood of movement*. The quality of the habitat matrix surrounding the habitat of pollinators strongly influences their movements (Kremen et al. 2007, Klein et al. 2008), and consequently the provision of pollination service (Westphal et al. 2003). Pollinators tend to move towards sites with equal or higher resources, we include this factor based on the quality of the surroundings of nesting sites. Likelihood of movement (M_x) was calculated as follows:

$$M_x = \frac{\frac{1}{n}\sum_{i=1}^{n} N_i}{N_x} \tag{1}$$

where N_x is the suitability score for nesting in a cell x, and N_i is the suitability score of the eight surrounding cells. The obtained values were adjusted between 0 and 1, if M_x >1, the outcome was converted to 1 (highest suitability). This means that, while the possibility of movement towards any of the pixels of the matrix remains, each pixel has a different probability of being abandoned to perform foraging activities in the surrounding cells. The mean value calculated from surrounding cells indicates the quality of the matrix, which were used as an indicator of movement.

4) *Potential nesting sites*. The final value of the potential for nesting sites per cell (NS_x) was calculated as

$$NS_x = N_j \times M_x \tag{2}$$

where N_j is the suitability score to provide nesting and M_x the probability of movement towards neighbouring cells.

5) *Floral resources by land cover type*. As with nesting suitability, each land cover type from the GlobCover 2009 map was scored according to its potential to provide floral resources for pollinator feeding, from 0 (null potential) to 1 (highest potential). The floral resources scores (F_j, Table 3.1) were those suggested by Tallis et al. (2011), Zulian et al. (2013) and complementary literature (Roubik 1992, Boreux et al. 2013). For instance, water bodies were

assigned 0 potential to provide floral resources, while a mosaic of cropland-vegetation reaches a 0.75 potential. The influence of corridors was estimated in the same way as for nesting sites.

6) *Foraging distance*. Pollination depends on the distance between nesting sites and foraging sites. Pollination is possible if the distance between these sites is equal to or less than the pollinator's foraging range. Also, there is an exponential decrease in foraging activity as the distance from the nest increases (Abrol 1988, Gathmann and Tscharntke 2002, Zurbuchen et al. 2010), i.e. the probability of pollination is higher near the nest. Thus, the suitability of cell x and surrounding cells to provide floral resources was estimated dependent on the distance from the nests.

The estimation of pollinator's foraging distance was based on empirical data for six species of tropical bees, including solitary and social species (Appendix B: Table B.1). The data used for this estimation was retrieved from studies where the frequency of individuals recorded at various distances from the nest was explicitly reported for known tropical crop pollinators (Gary et al. 1972, Abrol 1988, Dyer and Seeley 1991, Walther-Hellwig and Frankl 2000, Greenleaf et al. 2007). A positive correlation between pollinator's body size and foraging distance has been identified, foraging distance increases as body length (Gathmann and Tscharntke 2002) or distance between wings increases (Greenleaf et al. 2007). Although our sample is small, it applies to bee species ranging from 8 to 26 mm in length.

The number of cases reported every 100 meters up to 4000 meters (95% of cases included) from the nesting site for each species, was converted to a percentage of cases. Then, this percentage was averaged to obtain a general distribution of cases depending on the distance. The percentage of occurrence of each species was calculated and averaged across all species every 100 meters for 4000m with significant numbers found only in the first 1500m (Appendix B: Fig. B.1). These percentages were used to obtain an exponential decay function

$$D = e^{-0.004x} \tag{3}$$

where x is the distance in meters from the nesting site. The constant of decay (-0.004) was calculated as the mean difference between the proportion of cases every 100 m away from the nest. Thus, D was used to weigh the suitability to provide floral resources, where nearby cells have higher values than distant cells.

Since cell size is 300 m, D was calculated every 300 m up to 1500m from cell x. A kernel weight (D) was applied in an 11x11 matrix where cell x (at the centre of the matrix) weighted 1, and surrounding cells had an exponentially decreasing weight (Appendix B: Fig. B.1). The output for cell x is the mean value of the suitability score of this and surrounding cells after applying the weight value.

7) *Potential foraging sites*. The suitability value to provide floral resources of cell x was calculated as

$$FR_x = \frac{\sum_{i=1}^{n} F_j D_i}{n} \tag{4}$$

where F_j is the suitability score to provide floral resources, D_i is the weight value depending on the distance from cell x, and n is the total number of cells.

Once the suitability of cell x to provide nesting sites (NS_x, eq 2) and floral resources (FR_x, eq 4) was calculated, it was possible to calculate the pollinator abundance (Pa) as the product of these two components,

$$Pa_x = NS_x \times FR_x \tag{5}$$

8) *Barriers*. There is contrasting evidence regarding the influence of rivers, roads and railways on pollinators (Wojcik and Buchmann 2012). While marginal habitats represent a potential refuge in highly-altered landscapes (Potts et al. 2016), evidence suggests they can act as barriers in barely-modified habitats. In this scenario, pollinators tend to avoid the edges created by roads, railways and rivers (Ricketts 2001, Bhattacharya et al. 2003, Kremen et al. 2007). They can cross them, however, these structures may alter their movement depending

on the magnitude of the barrier, innate site fidelity and differential foraging behaviour among species and individuals (Rasmussen and Brødsgaard 1992, Ricketts 2001, Bhattacharya et al. 2003).

The data used comprises major roads (primary routes), rivers (perennial, Strahler stream order >2) and railways (FAO 1997b, a, 2014b), therefore, they were considered as potential barriers. Thus, their density per pixel (m/m2) was calculated for all the pixels without alteration by agriculture. The relative density of barriers in the study area was calculated as a proportion of the maximum density value in the study area. Finally, the difference from 1 was calculated (i.e. suitability = 1 - relative density of barriers in cell x) to be multiplied by the potential abundance scores (Pa_x, eq 5). This means that, although pollination can occur in the presence of these barriers in non-agricultural areas, the probability increases in their absence.

9) *Activity*. Insect activity is strongly dependent on ambient temperature (Mellanby 1939, MacMillan and Sinclair 2011). Foraging activity, and consequently pollination effectiveness, is null if the pollinator’s body temperature is below 10°C and increases as temperature rises above this threshold (Corbet et al. 1993). Corbet et al. (1993) developed a model to estimate insect temperature, calculated as a function of ambient temperature T (°C) and solar radiation R (W·m-2):

$$T_{bg} = -0.62 + 1.027(T) + 0.006(R) \tag{6}$$

where T_{bg} is the temperature of a black spherical model used in their experiments. Based on this, Zulian et al. (2013) suggest an annually-averaged activity coefficient (A), given as a percentage, to represent pollinators’ activity. The activity coefficient is calculated as:

$$A = -39.3 + 4.01(T_{bg}) \tag{7}$$

To calculate the activity coefficient in the study area, first, solar radiation for a completely clear sky was calculated using the Area Solar Radiation tool (ESRI 2015), derived from a DEM

(Jarvis et al. 2008). This was calculated independently for each degree of latitude (35 to -35), accumulated for a year. The output radiation rasters have units of watt-hours per square meter (WH·m-2). To obtain initial solar radiation under clear sky (R_0), these were divided by the number of daylight hours per year. Daylight hours were calculated using the model of Forsythe et al. (Forsythe et al. 1995) as a trigonometric function of latitude (Appendix B: Table B.2). The amount of initial solar radiation (W·m-2) was then adjusted using the mean annual cloud frequency (Wilson and Jetz 2016). The final solar (R) radiation raster was determined by using clear sky insolation and the fraction of cloud cover using the equation of Ashrafi et al. (2012)

$$R = R_0(1 - 0.75n^{3.4}) \tag{8}$$

where R_0 is solar radiation (W·m2) and n is the percentage of cloud cover.

Secondly, T_{bg} (eq 6) was calculated using the final solar radiation raster and WorldClim mean annual temperature data (Hijmans et al., 2005). Finally, the pollinators' activity coefficient (A, eq 7) was calculated through the study area. Those values <0% or >100% were adjusted to 0% and 100%, respectively (Zulian et al. 2013).

10) *Potential pollination*. The potential pollinators' abundance (Pa), the density of barriers (B) and the activity index of pollinators (A) were used to estimate the potential provision of pollination service (Pp) as $Pp = \ Pa \times B \times A$.

Realised pollination

To model realised pollination, i.e. where service is used, the occurrence of tropical crops for which insect pollination is essential or very important was considered (Roubik 1995, Klein et al. 2007). We followed the same procedure as that used to model potential pollination, but foraging sites were restricted only to the areas where pollinator-dependent crops were distributed, according to the 'Geographic distribution of major crops across the World' map

(Leff et al. 2004). Under the category 'Other crops' are included highly dependent nuts, fruits, vegetables, spices and oil-bearing crops (Appendix B: Table B.3).

The foraging suitability score (F_j) was transformed to zero in all those cells that did not overlap or were not within foraging distance to pollinator-dependent crops, the remaining cells kept their original values. A 1500 m buffer was added to this distribution, to include pollinators from nearby nesting sites. This distance based on the observations used for the foraging distance variable. The overlapping cells kept their original foraging suitability score. Thus, floral resources other than the distributed in the pollinator-dependent crop range were excluded.

Thus key modifications to the currently available models (Lonsdorf et al. 2009, Zulian et al. 2013) are the estimation of the likelihood of movement from nesting sites given the suitability of adjacent sites to account for the effect of land cover in bee movement; the calculation of a probability of foraging distance to reflect the decrease in pollination activity with the increase of distance from the nest (particularly important for solitary species, Klein et al. 2008), to represent more accurately process compared to the use of a mean distance value like the suggested for other models; finally, the role of major barriers was also considered in this model.

3.2.1.3. Pollination service to crops within protected areas

We used the realised pollination model results to estimate how much of the service provided to crops is currently within protected tropical forests. We summed the values of the cells across the study area to calculate the total value of potential and realised pollination. Then, we summed the values within PAs polygons. Thus, we calculated the percentage of the total service contributed firstly by all PAs globally, and then the contribution of each PA. To account for the PA size and estimate the density of service provision per PA, we divided the total service value of each PA (i.e. the sum of values within each PA polygon) by their respective area (sum/km^2). Thus, for each PA we provide a percentage of the total contribution to service provision and a density of service provision.

3.2.2. Results

The potential pollination map (Fig. 3.3a) shows the capacity per cell to provide pollination service regardless of the occurrence of crops. The values range from 0 (null capacity) to 0.494 (maximum capacity). The highest values are found in the Dry Chaco and Central Amazon Basin moist forests in South America; the Madagascar deciduous forests and Eastern Coastal moist forests in Africa; as well as dry evergreen forests in Sri-Lanka and Central Indochina dry forests in Asia.

The realised pollination map shows provision to pollinator-dependent crops (Fig. 3.3b). PAs with high potential to provide pollination that currently do not provide a service to agriculture show a null capacity of provision in this map. The regions with higher realised service are: in America, the South-eastern Mexican forests, the Central American Atlantic moist forests, Northern Dry Chaco and Central Amazon Basin moist forests; in Africa, Guinean forests, Madagascar's deciduous forests and Eastern Coastal moist forests; and in Asia, Central India deciduous forests, Sri-Lanka dry evergreen forests, Central Indochina dry forests, East Sumatra forests and South Borneo forests.

A total of 8,127 PAs located within the tropical forest ecoregions were included in the analyses. Together, these PAs protect over 20% of the area (~526,570 of 26,610,100 km^2). Approximately 60% (4,822) of these PAs are assigned to one of the six IUCN protected area categories (I=823, 10.1%; II=849, 10.4%; III=146, 1.8%; IV=966, 11.9%; V=816, 10.0%; VI=1,222, 15.0%) and 40% (3,305) are not reported/assigned. Categories I, II and III include natural areas that have not been modified permanently by humans, while categories IV, V, VI include areas with diverse semi-natural systems, including agricultural land (Dudley 2008).

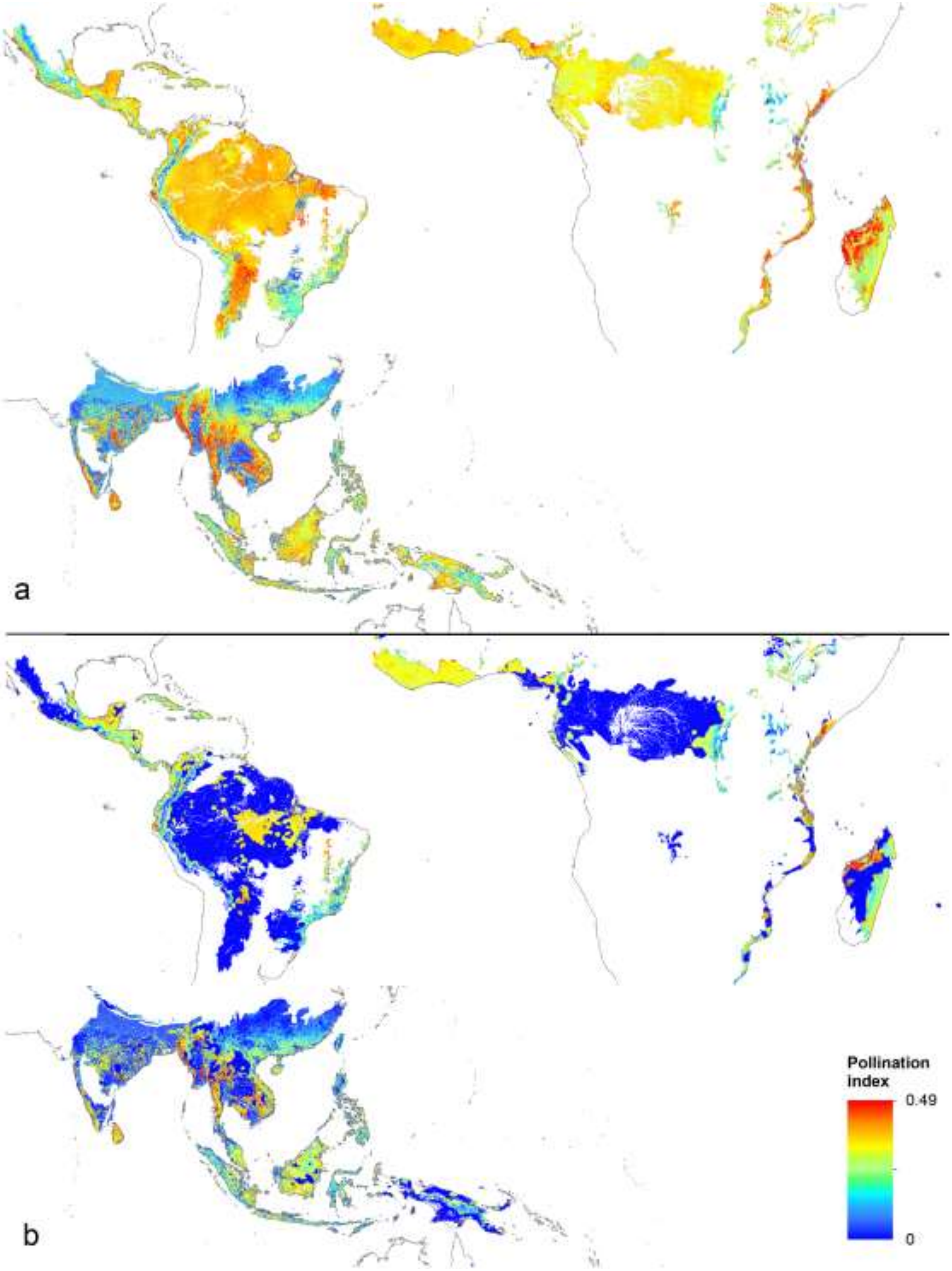


Figure 3.3. Pantropical pollination map. a) Potential pollination map shows the relative capacity per cell (300 m) for wild forest-dwelling bees to provide pollination, regardless of the occurrence of crops. b) Realised pollination map shows the capacity per cell to provide pollination to pollinator-dependent crops.

The sum of potential pollination values across the study area (4,094,178.6) and within PAs (872,451.5) indicated that 21.3% of potential service occurred in protected land. Regarding the protection of realised pollination, 80% of the PAs (6,480) contributed to the service (i.e. values >0), while 1,674 PAs had no contribution value(i.e. no realised pollination within these PAs). Equally, the sum of realised pollination values across the study area (2,032,447.1) and within PAs (319,116.1) indicated that 15.7% of service to crops occurred in protected land.

Of the total pollination service provided by PAs, the PAs with the highest absolute contribution (>1.0%) are in the American tropical forests (Fig. 3.4a): Kaa-iya del Gran Chaco, Bolivia (2.2%), Kayapó, Brazil (2.0%), Parque Nacional Do Jaú, Brazil (1.4%), Maya, Guatemala (1.2%) and Munduruku, Brazil (1.2%), adding 7.9% of the total sum of realised pollination values within PAs. When we plotted the PA area against their PA total contribution, we found that some of the largest areas had a lower contribution than some small or medium-sized PAs: Yanomami, Brazil (94,827 km^2, >0.01%), Vale do Javari, Brazil (86,244 km^2, 0%) and Alto Rio Negro, Brazil (80,059 km^2, 0.3%).

Regarding the estimation of the average value per km^2 (sum/km^2), small-sized PAs had higher sum values than medium- or large-sized PAs (Fig. 3.4b). The PAs with the highest per-unit contribution were: San Francisco, Mexico (PA area: 0.008 km^2; average value per km^2: 2.19); Luis Espinosa, Mexico (0.011 km^2; 1.78); San Carlos, Mexico (0.011 km^2; 1.26);. Zona de Conservación de Puerta del Mar, Mexico (0.026 km^2; 1.09); Weherebendikele, Sri Lanka (0.028 km^2; 0.91); and Area De Relevante Interesse Ecologico Parque Ambiental Antonio Danubio Lourenco Da Silva, Brasil (0.037 km^2; 0.75).

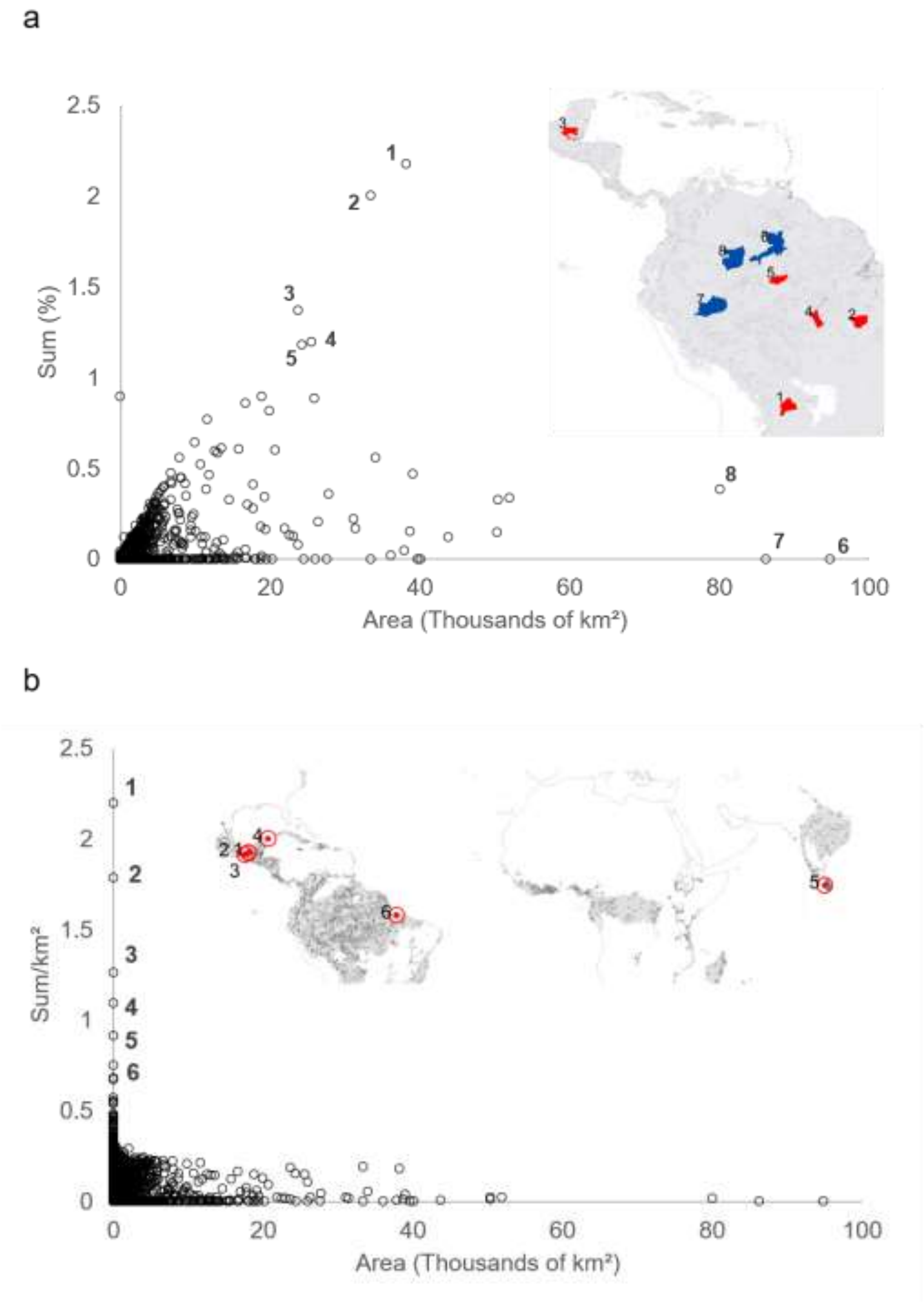


Figure 3.4. Contribution of protected areas to pollination service. a) Percentage of the total contribution of protected areas (PAs) against their size (km^2): 1. Kaa-iya del Gran Chaco, Bolivia, 2. Kayapó, Brazil, 3. Parque Nacional Do Jaú, Brazil, 4. Maya, Guatemala, 5. Munduruku, Brazil, PAs with the highest contribution in red and largest PAs with the lowest contribution in blue. b) Average per-km^2 contribution (sum/km^2) of PAs against their size (km^2): 1. San Francisco, Mexico (0.008, 2.19), 2. Luis Espinosa, Mexico (0.011, 1.78); 3. San Carlos, Mexico (0.011, 1.26); 4. Zona de Conservación de Puerta del Mar, Mexico (0.026, 1.09); 5. Weherebendikele, Sri Lanka (0.028, 0.91); 6. Area De Relevante Interesse Ecologico Parque Ambiental Antonio Danubio Lourenco Da Silva, Brasil (0.037; 0.75).

3.2.3. Discussion and conclusions

Protected pollination

PAs are a cornerstone to conserve tropical biodiversity (Laurance et al. 2012) and the regulating services biodiversity provides. The long-known Single Large Several Small (SLOSS) debate around the most effective size of PAs for biological conservation (Tjørve 2010) has now extended to ecosystem services (Eigenbrod et al. 2009). As for biological conservation, the optimal spatial configuration for PAs varies depending on ecosystem services conservation outcomes.

An assertion about the occurrence of regulating services is that these occur at a maximum in nonhuman-disturbed ecosystems (de Groot et al. 2010, Cimon-Morin et al. 2013). This is the case of services that operate at broad scales such as carbon sequestration and air purification (Hein et al. 2006), where the beneficiaries of the service do not require proximity to the source. Animal pollination, like other faunal regulating services (Gutierrez-Arellano and Mulligan 2018), operates at ecosystem scale (Hein et al. 2006), therefore, beneficiaries need to be close by where function takes place. Insect pollination of crops necessarily involves human-disturbed ecosystems. This is a clear example of how ecosystem services depend on a fine balance between human disturbance and nature conservation.

In this context, insect pollination of crops essentially depends on the proximity of crops to the source, in this case, natural areas (Kremen et al. 2004). Hipólito et al. (2019) showed the high value of PAs for crop pollination in Brazil. This is also observed at pantropical scale. The fundamental reason why the smallest PAs turn out to be the higher providers of pollination is their proximity to cropland. When the condition of occurrence of pollinator-dependent crops was included in the model, some of the largest PAs, usually located in areas isolated from human-modified ecosystems, were no longer a source of service. The PAs that contribute most to pollination provision per unit area are those containing or surrounded by a high density of agricultural land. The weight given by the distance factor increased the value of these PAs given their proximity to cropland.

Currently, some PAs do not contribute to crop pollination. Although these areas could contribute in the medium or long-term if agriculture expands near or within these areas, as suggested by the potential pollination model, it is imperative to highlight the relevance of these areas to provide suitable other species and services (e.g. water, carbon sequestration, Mulligan 2015b). Larger-sized PAs normally capture a greater range of environmental variation, hence a larger number of species across all taxa, and are more likely to support viable populations maximizing the community capacity of ecosystems and preventing or slowing down species extinction (Economo 2011, Durán et al. 2016). They also provide habitat for wildlife providers of other regulating services (e.g. natural pest control and seed dispersal, Gutierrez-Arellano and Mulligan 2018).

On the other hand, evidence suggests that small areas of suitable habitat can support diverse insect pollinator populations (Ricketts 2004), providing pollination to natural systems and crops. Smaller PAs tend to suffer more intense human-induced edge effect (i.e. the decrease in population sizes of some species at the interface between two land cover types, Mahmoudi et al. 2016), a higher pressure due to human activities and tend to be more isolated from other PAs or undisturbed ecosystems than larger-sized PAs (Parks and Harcourt 2002). Brosi et al. (2007) found a very significant difference in bee community composition at forest edges as compared to deforested farmland only a few hundred meters from forest. We suggest these factors be considered in PA management decisions in mixed forest-agricultural landscapes.

PAs located in American tropical forests showed the highest (absolute and proportional to size) contribution to crop pollination. Currently, PAs in this part of the world play a main role in safeguarding tropical biodiversity and ecosystem services (Naidoo et al. 2008). Also, in this part of the world, the highest deforestation rates are currently recorded (Aide et al. 2013, FAO

2015), as a result of the increase in intensive agriculture for exportation (Geist and Lambin 2002, Grau and Aide 2008). Deforestation, pollinator population loss and cropland expansion are a vicious cycle. Aizen et al. (2009) modelled the potential expansion of cropland and the resultant decline of pollinator populations. They estimate a decrease of 8% in agricultural production due to loss of pollinator populations and predict an increase in cultivated area, mainly in the tropics. Conservation of areas with the most suitable conditions to support pollinators' habitat and proximal to highly pollinator-dependent crops is essential to break this negative feedback.

Evidence suggests that pollination by wild bees contributes to crop production in areas where there is a mosaic of crops and adjacent remnants of natural and seminatural habitats that offer suitable nest sites (Klein et al. 2007, Ricketts et al. 2008, Aizen and Harder 2009). Areas of low to moderate agricultural intensification, such as subsistence agriculture or agroforestry, usually are more benefited by wild pollinators, while intensive commercial agriculture usually requires managed pollinators (Aizen and Harder 2009). Both, wild and managed pollinators have globally significant roles in crop pollination, although their relative contributions differ according to crop and location (Potts et al. 2016).

High dependence on managed pollinator species can have detrimental effects on natural systems. Managed pollinators can be competitors of wild-pollinator species and pollinate inefficiently native plants (Torné-Noguera et al. 2016, Geslin et al. 2017), they may act as pathogen transmitters, threatening wild-pollinator populations (Fürst et al. 2014), and may reduce the resilience of the pollination service to other environmental changes (Senapathi et al. 2015a). Therefore, focus on conserving or providing suitable habitat for wild pollinators is recommended for agricultural land near natural habitats, since this can enhance the benefit for both agro- and natural systems (Garibaldi et al. 2013), while integrated management of wild and domesticated species is recommended for commercial agriculture (Garibaldi et al. 2013, Potts et al. 2016).

In addition to assessing the relevance of PAs for the provision of pollination services, the model can be used to assess the pollination potential in agricultural land given the occurrence of non-protected natural habitat at a pantropical scale, and provide an insight on the optimal spatial configuration of semi-natural habitat.

Pollination model

Spatial modelling is a useful tool to synthesize and quantify the understanding of ecosystem services (Costanza et al. 2017). This model gives an initial approach to quantify and assess the distribution of pollination service at pantropical scale. This can be useful to identify sites with potential to be conserved given their pollination value or to locate pollinator-dependent crops, maximizing productivity and potentially reducing the extension of cropland.

This is the first step to further development of other models of regulating services provided by wildlife. By focusing on a single ecosystem service we might reduce the overall value relative to that for a full range of services (Costanza et al. 2017). Instead, the modelling of a bundle of services (InVEST, Tallis et al. 2011, ARIES, Villa et al. 2014, e.g. Co$ting Nature, Mulligan 2015b), can help to maximize the benefits obtained through time and space (Bhagabati et al. 2014, Mulligan 2015a), however, the level of detail for individual services is reduced. There is a trade-off between data collection and processing time and level of model detail and the number of services that can be modelled. The availability of multiple models for the same service allows comparison and thus assessment of model and data uncertainties and ensemble approaches to ecosystem service assessment.

Modelling allows assessing shifts in ecosystem services under different scenarios (Kubiszewski et al. 2017). By using land use and cover change models, this pollination model can assess potential changes in provision under different scenarios of conversion, such as conversion to agriculture in the absence of PAs.

Although models are valuable tools, uncertainty and limitations associated with them must be considered when interpreting the results (Oreskes 2003). The approach used to design the foraging distance equation in this model represent more accurately the effect of distance from nesting sites on pollination provision and provides robust results considering the available information. However, the limited data available is a source of uncertainty and can be subject to improvement. Small-sized stingless bees and solitary bee species are the most abundant flower visitor of tropical crops, such as coffee and cacao (Klein et al. 2008). Therefore, a better representation of these taxa in the calculation of the foraging distance variable is desirable.

At a local scale, Lonsdorf et al. (2009) validate their model with a moderate to a strong relationship between predicted and observed abundance values (R^2=0.5-0.8). Compared to other sites (California and New Jersey, USA), the fit is particularly strong for Costa Rica (R^2=0.8), showing the model is appropriate for tropical conditions. Although we cannot generalize this throughout the tropics, the environmental assumptions on which our model was built are justified. Validating the model at larger geographical scales would require tailored sampling since currently available data on pollinator abundance is insufficient and/or biased (Zulian et al. 2013). Validation should include other tropical regions, to assess if the role of corridors compares with that suggested for Europe (Zulian et al. 2013) and whether landscapes predicted as wild-bee scarce have crop pollination deficit.

Unlike temperate forests, where seasonality is noticeable, and mostly determined by temperature, the phenology of tropical forests is dominated by interspecific adaptation (Reich 1995), resulting in a staggered availability of resources throughout the year (Girardin et al. 2016). Therefore, seasonal variation in floral resources was not considered in this model.

It is worth mentioning that the model does not consider metapopulation dynamics, and therefore cannot evaluate whether these populations are sustainable in small forest fragments. The importance of small-sized PAs is based on their suitability to support pollinators without considering population dynamics over time.

An important factor that has not been considered in this model is the effect of pesticides on pollinators (Geiger et al. 2010, Isenring 2010). Currently, the global data on pesticide use is spatially coarse and assumes a uniform distribution of pesticide per country (Vorosmarty et al. 2010). The effects of this assumption on the model performance will require further assessment.

Equally, climate change has been identified as one of the main threats to wild pollinator populations (Schweiger et al. 2010). Changes in range, abundance and foraging activity have been observed as responses of climate change over the last decades (Chen et al. 2011, Kerr et al. 2015), and the overall reduction of habitat has been projected for some species (Giannini et al. 2012). The effects of climate change could be incorporated in the pollination model using alternative climatic data and scenarios (e.g. van Vuuren et al. 2011). Modification of climatic data would have a direct influence on the foraging activity variable, given its relationship with temperature and solar radiation. Similarly, climate change may alter significantly distribution plant taxa (Shafer et al. 2015) and thereby major vegetation cover types (i.e. tree, herb, bare, Notaro et al. 2007), modifying the distribution of nesting and foraging sites of wild bees. Future work includes assessing the effects of land cover and climate change on pollination service in the tropics.

Finally, data on pollinator diversity is scarce and geographically biased, therefore a modelling approach to identify patterns of pollinator richness can be useful (Hofmann et al. 2017). Future work includes assessing the role of species richness in the model outcome.

3.3. Conclusion

A pantropical, spatially explicit model of pollination, derived from open-access global datasets, has been developed. This model is relevant from the regional to the global scale, given the spatial resolution and extent at which the analyses were carried out. The estimation of potential and realised service is relevant to assess current (realised) benefits for tropical crops, but also to assess the (potential) benefit in the future and/or its interaction with other ecosystem services and biodiversity.

The assessment of the current state of pollination service present within protected areas (protection) shows the importance of these areas in sustaining the services and the utility of the ES spatial models in ecosystem management decisions. The inclusion of FES is important to conserve and manage benefits provided by protected areas given the projected increase in demand for these services and the fact that they have a different causality and distribution to many other services.

4 Effects of agriculturalisation on the distribution of supply and demand for pollination service in the tropics

4.1. Introduction

Land cover, land use and land cover and use change

Land cover is defined as the observed bio-physical cover on the earth's surface, e.g. vegetation type and man-made features. While the land use concept refers to how and/or for what purpose humans use the land. Thus, land use is defined by the land cover and the actions of people in their environment (Di Gregorio and Jansen 2005). For instance, 'tree cover' is a land-cover term, while 'native forest' and 'tree plantation' describe its use.

Land cover change can occur due to natural phenomena, e.g. fires, landslides or floodings, and can involve a subsequent recovery towards pre-phenomena conditions (Brown et al. 2012). While land use and cover change (LUCC) necessarily involves the transformation of the original cover by humans and usually implies a sustained change in management following the land cover change, e.g. clearing forest for agricultural use (Watson et al. 2000).

LUCC is considered the main factor of loss, modification and fragmentation of habitats, causing biodiversity loss and ES degradation by reducing carrying capacity and functioning of some ecosystems (Gaston et al. 2003, MA 2005).

Turner et al. (1995) identify three dimensions of LUCC drivers: socio-economic (e.g. technology development, economies), biophysical (e.g. soil degradation) and modalities of land management (e.g. cultural practices). These influence LUCC at different spatial and temporal scales (Verburg et al. 2004). To understand the impact of LUCC on a given natural system is necessary to identify the relevant drivers in a specific spatiotemporal scale. Although LUCC often occurs at local scales, as this practice has intensified and extensified, it has generated global consequences (Foley et al. 2005, Newbold et al. 2015).

Goldewijk et al. (2017) estimate the extent of human-induced LUCC up to 10,000 years ago by using demographic growth, cropland and induced pastureland data and using a modelling approach (History Database of the Global Environment, HYDE). They estimate that the global human population has grown from approximately 4.4 million to 7.257 billion in the last 10,000 years. The industrial revolution has been suggested as the start of Anthropocene (first signal of humankind causing global-scale changes in atmospheric conditions), although early dates have been proposed (Lewis and Maslin 2015). From the early eighteenth century until the present, global cropland area has increased more than five times (293 to 1,591Mha, uncertainty range 1,572-1,604 Mha), global pastureland more than six times (1,192 to 3,241 Mha, uncertainty range 3,211–3,270 Mha, Goldewijk et al. 2017).

As a general trend, in the past, most of LUCC occurred in natural grasslands and to a lesser extent in forests globally. There has been variation among regions and periods. Temperate regions of developed countries had the major changes during the nineteenth century, while most of tropical developing countries have faced the largest LUCC since the late twentieth century to the present (Song et al. 2018). Currently, tropical forest lands present the highest rates of LUCC (FAO 2015).

Forest and deforestation

There are several hundred official definitions of forest (Lund 2018), some of them rely only on biophysical properties, while others include intended use. For instance, the United Nations Food and Agriculture Organization Forest Resources Assessment (FAO 2015) defines forest as ‘land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 %, or trees able to reach these thresholds in situ. It does not include land that is predominantly under agricultural or urban land use'.

The United Nations Framework Convention on Climate Change (UN-FCCC 2002) suggests this definition: 'A minimum area of land of 0.05–1.0 ha with tree crown cover (or equivalent stocking level) of more than 10–30 % with trees with the potential to reach a minimum height of 2–5 m at maturity in situ. A forest may consist either of closed forest formations where trees of various storeys and undergrowth cover a high proportion of the ground or open forest. Young natural stands and all plantations which have yet to reach a crown cover of 10–30 % or tree height of 2–5 m are included under forest, as are areas normally forming part of the forest area which are temporarily unstocked as a result of human intervention such as harvesting or natural causes but which are expected to revert to forest'.

These definitions, like many others, differ in the specific thresholds of area, tree cover percentage, tree height and magnitude of human intervention (Lund 2018). There is no unique correct definition, forests are defined, assessed and valued through different lenses depending on their intended purpose(Chazdon et al. 2016).

The definition of deforestation depends on the definition of forest, therefore, it is equally variable. This varies depending on the type of change assessed, these can include land-cover change, land-use change or both and can include time features (i.e. temporary or permanent, Sunderlin and Resosudarmo 1996). For instance:

The United Nations Food and Agriculture Organization Forest Resources Assessment (FAO 2000) defines deforestation as 'the conversion of forest to another land use *or* the long-term reduction of the tree canopy cover below the minimum 10 % threshold. Deforestation implies the long-term or permanent loss of forest cover and implies transformation into another land use. Such a loss can only be caused and maintained by a continued human-induced or natural perturbation'. While the United Nations Framework Convention on Climate Change (UN-FCCC

2002) defines deforestation as ‘the direct human-induced conversion of forested land to nonforested land’.Here, the definitions adopted are the ones suggested by Hansen et al. (2013), the authors of the Global Forest Change spatial dataset. This dataset was used to assess the effect of agriculturalisation on pollination services in the tropical forest of the world. Similar to the FAO (2015) definition, forest is defined as ‘vegetation taller than 5m in height and tree cover above 10%’. Deforestation, also denominated ‘forest loss’, is defined as ‘a stand-replacement disturbance, or a change from a forest to non-forest state, during the period 2000–2018’.

4.1.1. Deforestation in tropical forests

Deforestation is an indicator of LUCC trends. During the period from 1982 to 2016 global tree cover has increased by 2.24 million km^2 (+7.1%). This overall net gain is the result of a net loss in the tropics (−4.1%) being outweighed by a net gain in the extratropics, especially in temperate continental forests (+33%), partly due to natural afforestation on abandoned agricultural land and partly due to forestry management (Song et al. 2018).

The largest forest area loss occurs in tropical regions, home to the greatest biodiversity on Earth (FAO 2015, Song et al. 2018). This is occurring in a few localized areas (Fig. 4.1), the sites under greatest deforestation pressure per continent are: in Africa, Madagascar, Côte d’Ivoire, and Congo basin; in Southeast Asia, Sumatra, Borneo, Vietnam, Cambodia, and Myanmar; and in America, the Amazon Basin, Gran Chaco and Atlantic forest, Yucatán Peninsula and the Nicaraguan border with Honduras and Costa Rica (Lambin et al. 2003, Aide et al. 2013, Song et al. 2018).

Curtis et al. (2018) identified the recent drivers (2001-2015) of deforestation globally. Shifting agriculture and commodity-driven agriculture are the main causes in tropical forests. In Southeast Asian countries they identified widespread deforestation due to expansion of oil palm plantations. In Central and South America, forests were converted to row crop agriculture and cattle grazing lands. Finally, shifting agriculture was the dominant driver in sub-Saharan Africa.

Figure 4.1. World distribution of biodiversity hotspots. Two-thirds of the hotspots area (shaded) is distributed in the tropics (black). The highest rates of deforestation are occurring in a few localized areas within tropical biodiversity hotspots (stars).

The largest area of tropical forest in the world is in South America (Aide et al. 2013). This is recognized as an important region for ES production globally (Naidoo et al. 2008), however, this can be adversely affected given the high rates of LUCC. The countries with the largest area of net tree cover loss between 1982 and 2016 are Brazil (−8%), Argentina (−25%) and Paraguay (−34%, Song et al. 2018).

Simultaneously, afforestation (i.e. forest gain) has been reported in some areas of Central America (Grau and Aide 2008, Aide et al. 2013) and Central Africa (Aleman et al. 2018), although to a lesser extent than deforestation, due to agricultural land abandonment.

4.1.2. Land-use change models

LUCC models are useful tools to analyse the causes and consequences of land-use dynamics and to make informed decisions (Verburg et al. 2004). Several models have been described in the literature in multiple disciplines (e.g. landscape ecology, computer sciences, economics, etc.), each differing in goals, methodological approach, data availability, dimension and scale applied (Brown et al. 2012). All these factors produce a high variability in the outcomes produced by different LUCC models. For instance, in a comparison of 11 global-scale LUCC models, Prestele et al. (2016) identified LUCC type definitions and the individual model allocation of change schemes as the main causes of prediction variability.

Many reviews on LUCC models have been produced (e.g. Baker 1989, Agarwal et al. 2002, Verburg et al. 2004, Brown et al. 2012) using different typologies. The review by Kaimowitz and Angelsen (1998) refers to over 140 models of tropical deforestation available at the time. Here, regional-level models are grouped in three main categories: 1) analytical, the models are an abstract, theoretical construct, which exclude empirical data, and are expressed in mathematical equations; 2) simulation, where the models use parameters based on facts drawn from various sources to assess scenarios and the impact of changing such parameters; and 3) regression models, based on a set of statistical analysis to estimate the relationship between LUCC (response variable) and one or more explanatory variables (Kaimowitz and Angelsen 1998, Brown et al. 2007).

Many LUCC models are not spatially explicit, i.e. these do not answer the question where deforestation can occur. In contrast, spatial LUCC models provide information not only on how much forest is likely to be cleared but also on which specific locations have the highest risk of being deforested. The development of computers, geographical information systems and associated land cover data from remote sensing products, has allowed spatial factors to be included in deforestation models (Dezécache et al. 2017, e.g. Table 4.1). Spatially explicit models provide insights about forest fragmentation, land management, and biodiversity conservation, among others (Kaimowitz and Angelsen 1998).

4.1.3. Scenarios of land-use change

The spatial heterogeneity in driving factors —socioeconomic, biophysical and historical factors (e.g. table 4.1)—has led to spatially distinct land-use patterns. Several techniques can be used to understand the spatial relationship between historical changes in land use and its driving factors. Then, it is possible to project spatial changes in land use under different scenarios based on the variability of these drivers (Meiyappan et al. 2014).

Usually, LUCC scenario assessments are based on gradual changes in socio-economic conditions (e.g. population density, infrastructure development, agricultural productivity; Fuller et al. 2012), and biophysical or climatic conditions (e.g. soil quality, temperature change, extreme weather events; Carter et al. 2007). Many of them focus on local and regional issues, only a few are global in scope (Meiyappan et al. 2014), such as QUICKLUC.

LUCC scenarios assessments often include the 'business-as-usual' scenario (BAU), which assumes a non-significant change in rates, patterns and distribution of change, so that current trends can be expected to consistently continue through time. BAU scenarios are contrasted with scenarios where new actions significantly affect change rates, locations and patterns, such as implementation and enforcement of protected areas (e.g. Soares-Filho et al. 2006), or prioritisation of agricultural expansion over forest protection(e.g. Koh and Ghazoul 2010).

Table 4.1. Tropical land use change models. Examples of spatial land use change/ deforestation models developed for tropical regions, type (as described by the authors), biophysical (*) and socioeconomic (^) variables included in the models, and the sites where have been applied.

Model	**Type**	**Variables**	**Study site**	**Reference**
Geographical modelling (GEOMOD)	Spatial regression rule-based model[1]	*Elevation, slope, aspect, precipitation, temperature, distance to water bodies, soil, vegetation type ^Distance to roads, distance to human settlements, political districts	Southeast Asia Mexico (Chiapas, Campeche, Michoacán) Paraná, Brazil Santa Cruz, Bolivia	Hall et al. (1995), Brown et al. (2007)
Manson 2000	Agent-based dynamic model[2]	*Hydrology, soil type, slope, aspect, suitability for agriculture ^Land use type, suitability for agriculture, forestry and non-timber forest products, distance to market, transportation infrastructure	Yucatán Peninsula, Mexico	Manson (2000)
Messina and Wash 2000	Cellular automata model[3]	*Elevation, slope, hydrography, land cover type ^Land use type, distance to roads, (unspecified) socio-economic data	Ecuadorian Amazonia	Messina and Wash (2000)
CLUE-S	Dynamic model[4]	*Altitude, slope, aspect, distance to stream, erosion, geology ^Distance to roads, towns and ports, population density	Central America, Malaysia, Philippines	Verburg et al. (2002)
Dinamica EGO	Cellular automata model[3]	*Vegetation type, soil type, altitude slope distance to rivers, distance to deforested and forested areas ^Influence of population centres, distance to roads	Brazilian Amazonia, Colombia	Soares-Filho et al. (2013), Negret et al. (2019)
QUICKLUC 2.0	Equilibrium model[5]	*Forest cover ^Distance to deforestation fronts Accessibility to population centres Planned infrastructure	Africa, Asia, South America	Mulligan (2015b)

[1] The model is calibrated by assigning weights to map cells based on analysis of the importance of each of the variables and combination of them, it uses the kappa index for internal validation.

[2] The model combines an agent-based and a dynamic spatial simulation model to obtain an integrated assessment model based on three components: actors (agent), institutions and environment

[3] The model employs user-defined rules assigning one of a finite number of possible states (k) to each of the cells of a uniform grid, the state is updated by the interaction of rules.

[4] Designed for small regions, the model is based on systems theory, it addresses the hierarchical organization of land use systems, spatial connectivity and stability.

[5] This was the model selected to assess the effect of land use and cover change on pollination service. The model is explained in detail in section 4.2.1

4.1.4. Effects of LUCC on ES

Consequences of LUCC in tropical forest landscapes on ES have been explored recently, mainly in a study case basis (e.g. Ricketts et al. 2004, Grau et al. 2008, Martínez et al. 2009, Williams-Guillén and Perfecto 2010). The ecosystem services addressed in these studies include hydrological services (Grau et al. 2008, Martínez et al. 2009), pollination (Ricketts et al. 2004, Ricketts et al. 2008) and pest control (Williams-Guillén and Perfecto 2010). As a general conclusion, these studies suggest that larger forested areas and high landscape heterogeneity improve ES supply to agro- and urban ecosystems, while intensive and extensive livestock and agricultural activities have a negative impact. The understanding of the global effects of LUCC on ES could be improved by upscaling the analysis from the local to the regional and global scale, thereby understanding variation in responses within and between landscapes.

In this chapter, the effects of the conversion of forest to cropland, i.e. agriculturalisation, on pollination services in the tropics were assessed using the model of pollination distribution described in Chapter 3. The hypothesis tested in this chapters were:

1. The exclusion of deforestation in tropical protected areas would conserve potential and realised pollination services in the long-term.
2. The conversion of forest to cropland in highly forested areas would increase realised pollination in the short-term.
3. The most fragmented forest patches in the present would provide the highest realised service in the future due to an increase in the perimeter of the forest-cropland edge.

The QUICKLUC model (Mulligan 2015b) was used to generate two scenarios of change, conservation and non-conservation scenarios. These scenarios were projected forwards to assess the effects of change on service in the short (32 years) and long (200 years) terms.

Projected land cover maps were generated and used to model projected pollination distribution. The difference between present-day (i.e. baseline) and projected pollination distribution was calculated and its relationship with current fragmentation was assessed. This was first carried out regionally (i.e. Amazon, Gabon, Paraguay, Sri Lanka and Yucatan) and then pantropically.

4.2. Methods

4.2.1. QUICKLUC model

The LUCC model used to estimate the change in pollination provision is QUICKLUC (v2.1). This model is part of the web-based Policy Support tools WaterWorld and Co$ting Nature (Mulligan et al. 2010, Mulligan 2015b). Unlike other LUCC models, QUICKLUC is spatially explicit and globally applicable at variable resolution (1 ha, 1 km, 10 km). Some models perform specifically at a regional scale (e.g. Verburg et al. 2002, Soares-Filho et al. 2013), while others perform at a global scale at a coarse spatial resolution (e.g. IMAGE, 0.5-degree resolution, Dobrovolski et al. 2011). QUICKLUC can be applied from a local to a global scale at high-resolution (up to 1ha). This peculiarity allows the use of the same model to compare regional scenarios and carry out a pantropical assessment. This model is open access, all data required is supplied, its execution is easy, fast and has no software requirements. Furthermore, it allows detailed customisation by the user to simulate the land cover and use transitions of interest.

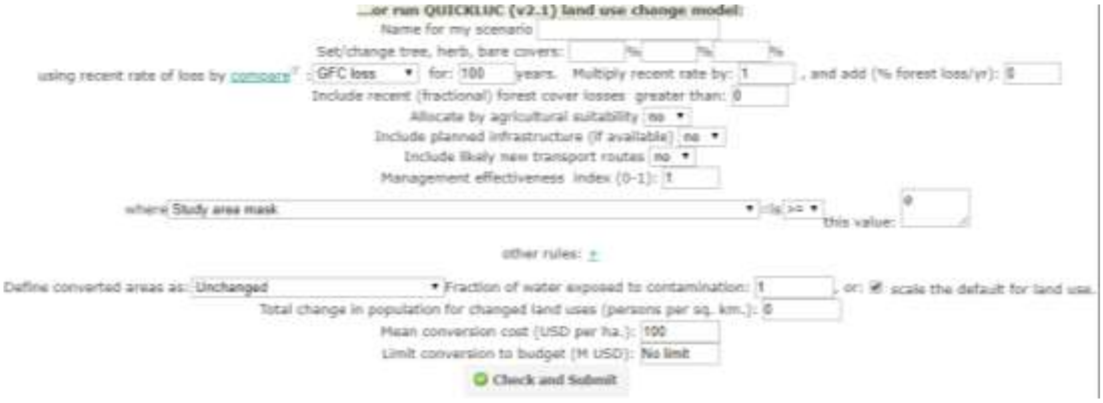
QUICKLUC is an equilibrium model, which projects a given future time in a single step without going through a series of intermediate time steps, only one time period is predicted per simulation. QUICKLUC projects deforestation based on recent rates estimated from three different datasets: Global Forest Cover (GFC, Hansen et al. 2013), Terra-i (Reymondin et al. 2012) and FORMA (Hammer et al. 2014), these rates can be used independently or combined.

Recent rates of deforestation are assessed per regional administrative areas according to FAO (2014a), these can be increased or decreased by the user to reflect changing global economic, population and market conditions in the study area. The model allows allocating deforestation in areas where it has not occurred recently by adding a user-defined rate to the measured base rate. These rates are then applied for a specified number of years. Thus, the number of pixels to be deforested in an administrative region is calculated by multiplying the rate by the number of years.

It is also possible to set per pixel fractional forest cover losses to avoid overestimation of deforestation by assuming all is clear-cut at the pixel resolution. This means a pixel can be projected as partially deforested under a user-defined threshold instead of only assigned 100% deforested pixels. In a range of 0 to 1, a high value will project forwards clear-cut full pixel deforestation only (i.e. 1 means projecting 100% deforestation in the pixels), while a lower value will also project part-pixel deforestation and forest degradation as is common in many landscapes. For instance, a 0.3 threshold value will project pixels deforested above 30%. Deforestation is allocated by pixel based on distance rules: the Euclidian proximity to existing deforestation fronts and accessibility to population centres (Mulligan 2015b). In addition to the distance rules, the user can allocate deforestation considering agricultural suitability using the IIASA GAEZ (Global Agro-ecological Zones) analysis (IIASA/FAO 2012). The GAEZ approach identifies crop-specific limitations of climate, soil and terrain resources in a consistent way based on empiric data. It utilizes the land resources inventory to assess all feasible agricultural land-use options and to quantify expected production of cropping activities relevant in a particular agro-ecological context, for specified management conditions and levels of inputs.

If available for the study area, the user can include planned infrastructure in the model settings. Likely new transport routes are calculated by connecting all existing urban areas with a road (Schneider et al. 2009) and the user can choose to add them to the deforestation fronts calculation (Mulligan 2015b). Simultaneously, deforestation can be excluded for certain areas fully or through a set management effectiveness index, where values range from null (0) to total exclusion (1) of deforestation in those areas. Along with the user-defined exclusion, deforestation is not allocated in already deforested areas (according to the chosen dataset) and in non-forests areas (tree cover <10%, DiMiceli et al. 2011).

Deforested areas are converted to a land-use type defined by the user, these are most suitable agriculture, most common agriculture locally or regionally, in proportion to current agriculture locally or regionally, all grazing, all cropping, all natural or all protected land. (Fig. 4.2).



...or run QUICKLUC (v2.1) land use change model:

Name for my scenario:

Set/change tree, herb, bare covers: % % %

using recent rate of loss by compare: GFC loss ▾ for: 100 years. Multiply recent rate by: 1 , and add (% forest loss/yr): 0

Include recent (fractional) forest cover losses greater than: 0

Allocate by agricultural suitability: no ▾

Include planned infrastructure (if available): no ▾

Include likely new transport routes: no ▾

Management effectiveness index (0-1): 1

where Study area mask ▾ is >= ▾ this value: 0

other rules: +

Define converted areas as: Unchanged ▾ Fraction of water exposed to contamination: 1 , or: ☑ scale the default for land use.

Total change in population for changed land uses (persons per sq. km.): 0

Mean conversion cost (USD per ha.): 100

Limit conversion to budget (M USD): No limit

Figure 4.2. QUICKLUC (2.1) model interface showing default settings. This model was used to generate two scenarios of land-use change to assess its effect on pollination service.

4.2.2. Scenarios and model settings

Two scenarios of change were produced for two different periods, short term (2018-2050) and long term (2018-2218). The first one is a conservation scenario, where deforestation occurs at the current rates but is excluded from occurring in current protected areas (C2050 and C2218). The second is a non-conservation scenario, where overall rates of deforestation are the same, but the network of protected areas is ineffective, therefore deforestation occurs within and outside protected land (NC2050 and NC2218).

The settings to model these scenarios are shown in Table 4.2. and detailed below. For both scenarios:

a) Set/ change was ‘tree: −100%’, this means deforestation per pixel can include up to 100% tree cover), while herb and bare cover were set to 0, remaining in the proportion they currently exist in the area, which means no land-use change was projected in land-cover areas defined as herb or bare.
b) The forest loss rate selected for the projections was the rate estimated from the GFC dataset (Hansen et al. 2013) since it covers the spatial extent of the study area. The rate can be multiplied to increase or reduce the current forest loss rates, in this case, this was multiplied by 1, assuming the current rates will remain in the future (i.e. no increase in BAU rate). The settings allow to introduce deforestation in sites where it is currently absent by adding a given percentage to the current rates, here, there was added 0% of forest loss (i.e. no additional deforestation in sites with no current BAU deforestation). Thus, these settings were based on the assumption that the current deforestation rate and patterns will occur without significant changes in the future.
c) The projected deforestation was restricted to pixels suitable for agriculture based on the GAEZ criteria, this was done by enabling the ‘allocation by agricultural suitability’option.
d) Likely transportation routes were considered.
e) The converted areas were defined as cropland. This based on the assumption that currently, the main cause of forest loss in the tropics is extensive agriculture, and this will occur only in areas suitable for agriculture.
f) Finally, for the management effectiveness index, a value of 1 excludes all allocated deforestation, following the exclusion rules in areas defined by the user (e.g. exclusion of deforestation in protected areas), whilst a value of 0 excludes none of the allocated deforestation, meaning that, even when the user specifies areas of exclusion,

management ineffectiveness would allow the allocation of deforestation in such areas. Here, the management effectiveness index was set to 1, to enforce the exclusion rule for the conservation scenario detailed below.

Table 4.2. QUICKLUC model settings to generate two scenarios of land use change: conservation and non-conservation, at one of two time periods: 2018-2050 (32 years) and 2018-2218 (200 years), considering one of three different fractional values of forest cover losses (0.1, 0.5, 0.7)

Settings	**Conservation**	**Non-conservation**
Name for my scenario	**2050_C_10**	**2050_NC_10**
Set/change tree, herb, bare covers (%)	−100, 0, 0	−100, 0, 0
using recent rate of loss by compare:	GFC_loss	GFC_loss
for (years):	**32 / 200**	**32 / 200**
Multiply recent rate by:	1	1
add (% forest loss/yr):	0	0
Include recent (fractional) forest cover losses greater than:	**0.1 / 0.5 / 0.7**	**0.1 / 0.5 / 0.7**
Allocate by agricultural suitability	yes	yes
Include planned infrastructure (if available)	no	no
Include likely new transport routes	yes	yes
Management effectiveness index (0-1):	1	1
where	**Protected areas**	**Study area mask**
is	**= this value: 0**	**>= this value: 0**
Define converted areas as:	All Cropping	All Cropping
Fraction of water exposed to contamination:	1	1
or scale the default for land use	ticked	ticked
Total change in population for changed land uses:	0	0
Mean conversion cost (USD per ha.):	100	100
Limit conversion to budget (M USD):	No limit	No limit

The fundamental difference between scenarios was that for the conservation scenario, deforestation was restricted to occur only outside protected areas. This was done by setting the option ‘where’ to ‘Protected Areas (IUCN and UNEP-WCMC 2017) = 0’, i.e. no deforestation will occur within the Protected Areas polygons provided by the World Database on Protected Areas (IUCN and UNEP-WCMC 2017). While for the non-conservation scenario, this was set to ‘Study area >=0’, allowing deforestation to occur anywhere in the study area, including within the protected area polygons. The management effectiveness for both scenarios was set to 1, excluding deforestation completely within protected areas in the conservation scenario, and allowing deforestation in any pixels that meet the rest of the criteria in the study area for the non-conservation scenario.

Regarding the fractional forest cover losses, three different values were used to capture different per pixel partial losses, i.e. each scenario was run three times. The values assigned were 10%, 50%, and 70% of forest cover loss (0.1,0.5 and 0.7, respectively). Thus, with a 0.1 fractional value, deforestation was projected to pixels where deforestation could replace over 10% of their tree cover. Equally, 0.5 and 0.7 values projected over 50% and 70% tree cover loss. These values were selected according to the threshold values used to categorize land cover types in the GlobCover map (Arino et al. 2010; see Table 3.1), thereby connecting land cover to the land use classification.

Some of the outcomes of the model are a projected percentage of forest cover map, and a difference (change) map of this projection with the baseline tree cover forest map (DiMiceli et al. 2011, Fig.4.3a-c). The difference map of each of the deforestation thresholds shows the pixels where deforestation above 10%, 50% (e.g. Fig 4.3d) and 70% was projected. Each of these maps were converted to a Boolean map (0, no deforestation; 1, deforestation; Fig. 4.4b). This was done by reclassifying all the pixel values above 0 (where there was a cover loss above 10%, 50% or 70%) as 1, and all the pixel values equal to 0 (where there was no projected forest loss), remained as 0. The three Boolean maps were summed to get a single deforestation map showing where the forest loss would occur above the 10%, 50% or 70% of the pixel area. The areas with projected deforestation above 70% are nested within the areas with projected deforestation above 50%, and these in turn within the areas with projected deforestation above 10% as shown in Fig. 4.4c.

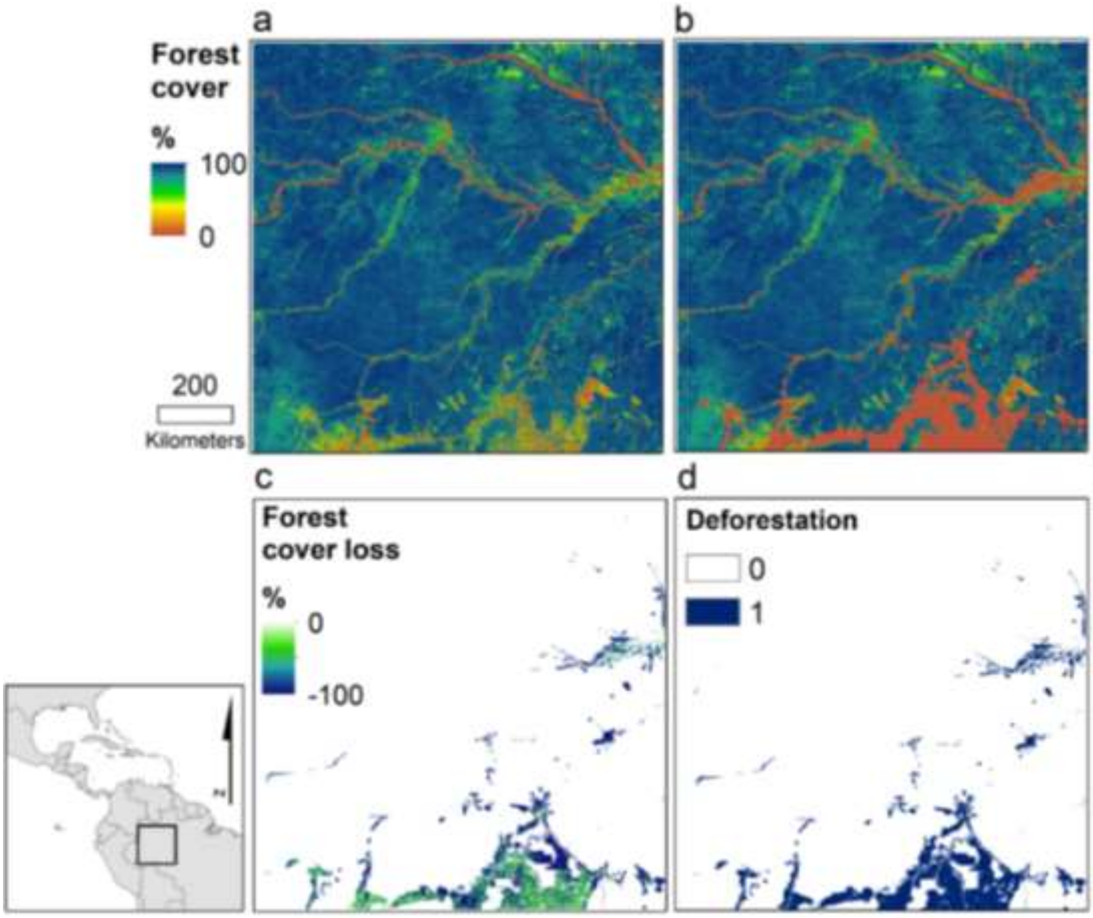


Figure 4.3. Projected forest cover in the Amazon. a) Baseline percentage of forest cover (DiMiceli et al. 2011), b) Percentage of forest cover projected (C2050), considering fractional deforestation >0.5, c) percentage of forest cover loss calculated as the difference of baseline and projected forest cover and d) Boolean map of projected deforestation occurrence. The a-c maps are QUICKLUC model outputs (Mulligan 2015b).

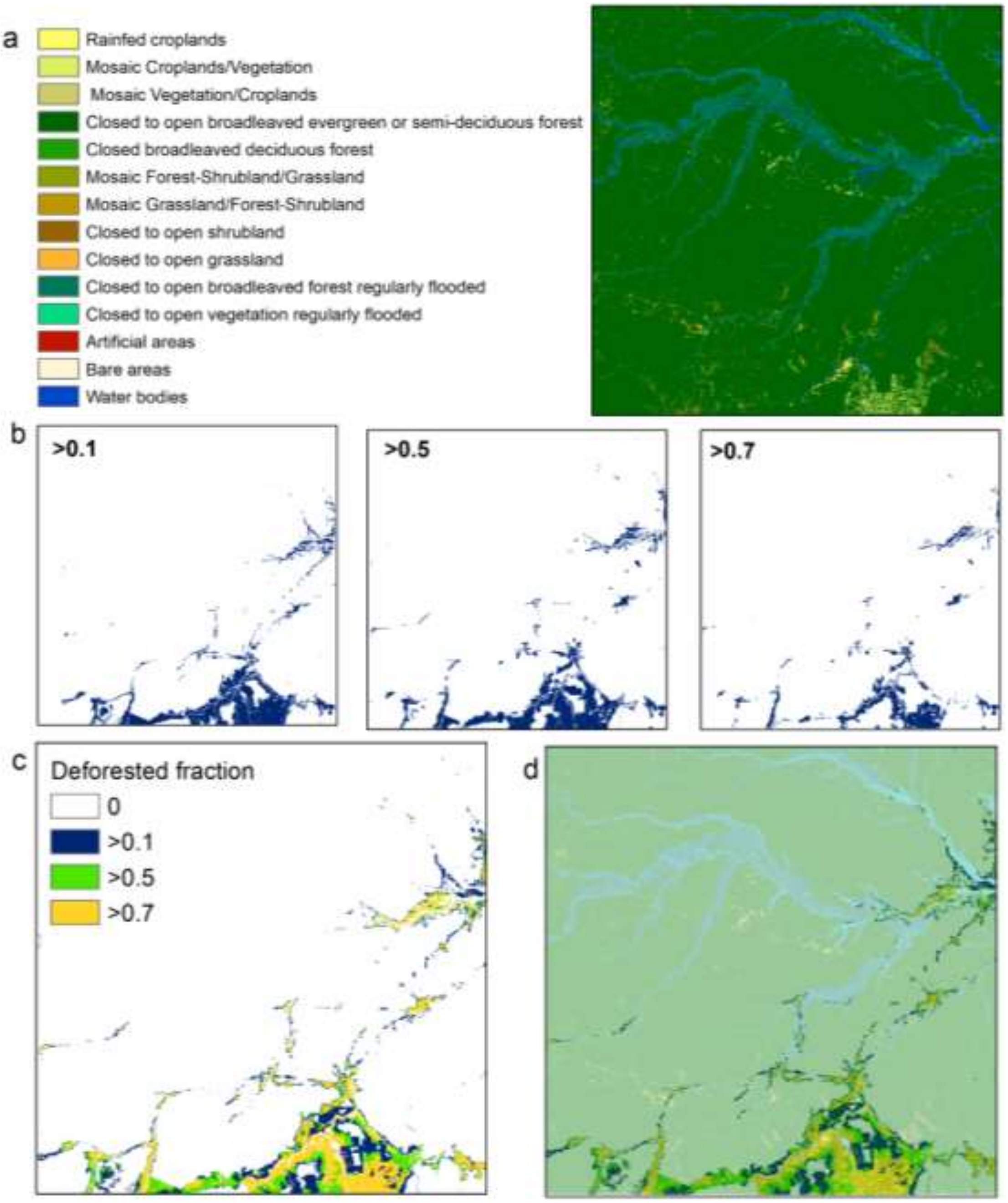


Figure 4.4. Intersection of current land cover types with projected deforestation in the Amazon (C2050). (a) GlobCover map (Arino et al. 2010) used to assign nesting suitability (N_j) and floral resources (F_j) scores for baseline pollination model. The QUICKLUC output maps of (b) projected deforestation occurrence under different fractional deforestation thresholds were combined to generate a single (c) projected deforestation map. (a) and (c) were intersected to identify the (d) areas where N_j and F_j were modified according to the projected percentage of forest loss.

Thus, the QUICKLUC model was run 12 times in total, for two scenarios, at two different periods, and considering three different fractional forest cover losses (Table 4.2) to obtain a projected deforestation map for C2050, C2218, NC2050 and NC2218. These runs were done regionally at 1 km resolution and globally at 10 km resolution.

4.2.3. Projected pollination

The projected deforestation maps were intersected with the GlobCover map (Fig. 4.4), to reclassify the nesting suitability (N_j) and floral resources (F_j) scores that were assigned to the current pollination model (Table 3.1). Under the GlobCover 2009 land cover type classification, the 'Mosaic vegetation' corresponds to a mix of natural vegetation and cropland with a higher percentage of forest/grassland/shrubland (50 -70%) and a lower percentage of cropland (20-50%); the opposite proportion (50-70% cropland; 20-50% natural vegetation) corresponds to 'Mosaic Cropland'; finally, a percentage >70% corresponds to 'Cropland'. Each of these land cover types has its respective suitability value to provide nesting sites (NS) and floral resources (FR):

- Mosaic vegetation: NS, 0.75; FR, 0.70
- Mosaic cropland: NS, 0.7; FR, 0.75
- Cropland: NS, 0.2 ; FR:, 0.2

Thus, depending on the original land cover type, the scores increased or decreased according to the projected percentage of forest loss per pixel (Table 4.3). For example, pixels currently classified as 'Broad-leaved deciduous forest' in the GlobCover map that when intersected with the projected deforestation map (e.g. Fig. 4.4c) showed 10%, 50% or 70% forest cover loss, changed their original suitability values to provide nesting sites (NS=0.8) and floral resources (FR=0.9) to those of Mosaic vegetation, Mosaic cropland or cropland respectively. Equally, in the case of pixels currently classified as 'Mosaic cropland,' a loss >50% implied conversion to 'Cropland' suitability values. Those pixels with no deforestation projected retained their original scores. For example, Table 4.4 shows the value conversion carried out for the Amazon region, under the conservation scenario by 2050 (C2050). Here, most pixels either lost between 10% and 50% of forest cover or above 70%, no deforestation was projected between 50 and 70% of forest loss for pixels assigned to certain land cover type according to the GlobCover map. For each region, the projected deforestation varied with the scenario (conservation or non-conservation) and the projection time (2050 or 2218). Therefore, the conversion tables, like the shown for the Amazon-C2050, differed for each scenario and region. Appendix C (Table C.1) shows a hypothetical reclassification table showing the values that were used to each land cover type depending on their projected forest cover loss.

Table 4.3. Criteria used to reclassify nesting suitability (N_j) and floral resources (F_j) according to the projected percentage of forest loss. Based on the GlobCover map percentage of cover type, the original N_j and F_j scores (0 -1) were reclassified per pixel to Mosaic vegetation (N_j: 0.75, F_j:0.7), Mosaic cropland (N_j: 0.7, F_j:0.75) and Cropland (N_j: 0.2, F_j:0.2). Pixels where no deforestation was projected retained their original score.

From	**To**		
	0.1- 0.5	**0.5 -0.7**	**>0.7**
Forest	Mosaic vegetation	Mosaic cropland	Cropland
Mosaic vegetation	Mosaic cropland	Cropland	Cropland
Mosaic cropland	Cropland	Cropland	Cropland
Spare vegetation	Cropland	Cropland	Cropland

These reclassified nesting suitability maps and floral resource maps were used to generate projected pollination maps following the same method to map current potential pollination (section 3.2.1.2). For realised pollination, the current cropland distribution was replaced by the projected distribution of cropland. Future cropland distribution was determined using the >50% forest cover loss map (i.e. cropland distribution using fractional deforestation value >0.5).

Projected pollination was first generated regionally (Amazon, Gabon, Paraguay, Sri Lanka and Yucatan) to assess the performance of the model under different regional deforestation rates and baseline conditions (five sites), and to analyse the possible effects of the LUCC scenarios. Then it was generated pantropically (averaged regional rates) to identify pantropical patterns of change.

Table 4.4. Reclassification table example: Amazon, 2050C. Nesting suitability (N_j) and floral resources (F_j) scores reclassified per pixel according to the projected percentage of forest loss. The deforestation thresholds were set to identify 10 to 50% (0.1-0.5) forest loss, 50 to 70% (0.5-0.7) forest loss and 70 to 100% (>0.7) forest loss per pixel. Pixels where no deforestation was projected maintained their original score (-).

ID	**GlobCover land cover type**	N_j				F_j			
		From	**To**			**From**	**To**		
			0.1-0.5	**0.5-0.7**	**>0.7**		**0.1-0.5**	**0.5-0.7**	**>0.7**
11	Post-flooding or irrigated croplands (or aquatic)	0.4	0.2	-	0.2	0.4	0.2	-	0.2
14	Rainfed croplands	0.2	0.2	-	0.2	0.2	0.2	-	0.2
20	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)	0.7	0.2	-	0.2	0.75	0.2	-	0.2
30	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	0.75	0.7	0.2	0.2	0.7	0.75	0.2	0.2
40	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)	0.8	0.75	0.7	0.2	0.9	0.7	0.75	0.2
50	Closed (>40%) broadleaved deciduous forest (>5m)	0.8	0.75	-	0.2	0.9	0.7	-	0.2
60	Closed (>40%) needle leaved evergreen forest (>5m)	0.8	0.75	-	0.2	0.3	0.7	-	0.2
70	Closed to open (>15%) mixed broadleaved and needle leaved forest (>5m)	0.8	0.75	-	0.2	0.6	0.7	-	0.2
110	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	0.9	0.75	-	-	0.9	0.75	-	-
130	Closed to open (>15%) (broadleaved or needle leaved, evergreen or deciduous) shrubland	1	0.75	0.7	0.2	0.9	0.7	0.75	0.2
140	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	0.4	0.2	-	0.2	0.4	0.7	-	0.2
150	Sparse (<15%) vegetation	0.35	0.2	-	-	0.7	0.2	-	-
170	Closed (>40%) broadleaved forest or shrubland permanently flooded	0	0	-	0	0	0	-	0
190	Artificial surfaces and associated areas (Urban areas >50%)	0.3	0.2	0.2	0.2	0.3	0.2	0.2	0.2
200	Bare areas	0	0	-	0	0	0	-	0
210	Water bodies	0	0	-	0	0	0	-	0

4.2.4. Quantification of change at regional scales

Five regions were selected through the study area (Fig. 4.5) to apply the QUICKLUC model and generate a projected distribution of pollination for C2050, NC2050, C2218 and NC2218. Sites were chosen to represent different combinations of climate, topography and rate/pattern of land-use change. The boundaries for these sites were specified using predefined polygons of the regions of interest provided by Co$ting Nature (Mulligan 2015b), the web-based tool where the QUICKLUC model is integrated. Administrative boundaries (countries) were selected for Gabon, Sri Lanka and Paraguay, drainage basin for Yucatan Peninsula (Yucatan) and a 10x10 degrees tile for the Amazon.

The regions differ in size, topography, main forest type and occurrence in biodiversity hotspot areas (biodiversity hotspots defined as areas with more than 1,500 endemic species of vascular plants and have lost >70% native vegetation, Myers et al. 2000) and recent deforestation rates (Table 4.5), assessed per regional administrative areas (FAO 2014a), comprising a variety of characteristics to apply the LUCC scenarios.

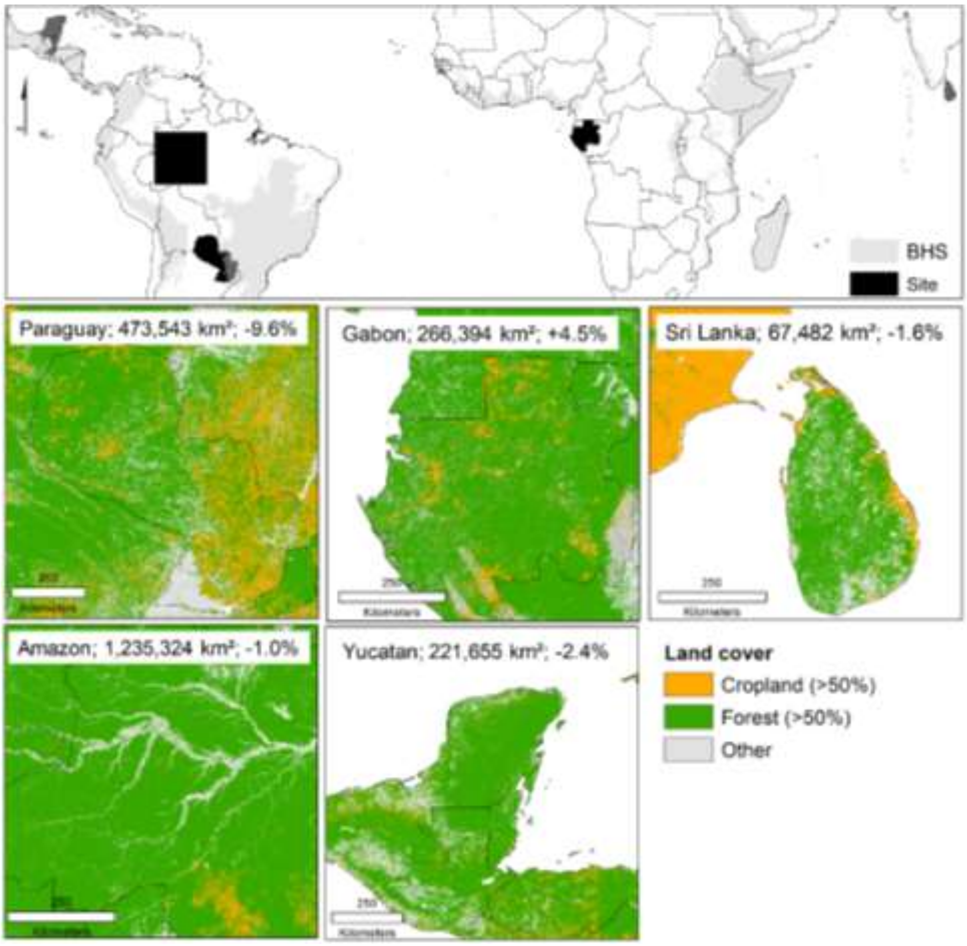


Figure 4.5. Sites where QUICKLUC and pollination models were applied (1 km resolution). Sites varied in area (km^2), topography, recent (2010-2015) forest cover loss/gain (%, FAO 2015) and occurrence in biodiversity hotspot areas (BHS, Myers et al. 2000).

Table 4.5 Selected sites to run the QUICKLUC model at regional scale. Sites varied in area, forest cover change (2010-2015) per country (Amazon: Brazil, Yucatan: average Mexico, Guatemala and Belize; FAO 2015), tropical forest type (NC 2012) and occurrence in biodiversity hotspot areas (BHS, Myers et al. 2000): yes (Y), no (No), partially (P).

Site	Area (km^2)	Cover change (%)	Forest type	BHS
Amazon	1,2135,324	-1.0	Moist broad leaf forest	N
Gabon	266,394	+4.5	Moist broad leaf forest	N
Paraguay	473,543	-9.6	Moist and dry broadleaf forest	P
Sri Lanka	67,482	-1.6	Moist and dry broadleaf forest	Y
Yucatan	221,655	-0.7	Moist and dry broadleaf, coniferous forest	Y

To assess the effect of LUCC on potential and realised pollination under the two scenarios, the following statistics were calculated for each site and each scenario:

a) Change in pollination service through time was calculated per site as the difference between the mean values of each projected pollination map ($\mu_{scenario}$) and the mean value of the current pollination map ($\mu_{baseline}$) of each site:

$$\Delta_{pollination} = \mu_{scenario} - \mu_{baseline}$$

b) Pollination change per unit of forest loss was calculated by dividing the mean pollination change of each site by the respective mean forest cover change, i.e. the difference between the baseline and projected forest cover of the site:

$$\text{Pollination change per unit of forest lost } = \frac{\Delta_{pollination}}{\Delta_{forest\ cover}}$$

Thereby it was possible to calculate the ratio of service change to forest loss, which allows comparison among sites. Three projected forest cover maps were generated per scenario (section 4.2.2), the forest cover map used for this calculation is the one derived from a fractional deforestation > 0.5.

c) The relationship between baseline forest fragmentation with projected pollination change per region was evaluated.

The edge effect can have a negative impact on the abundance of pollinators (Gutierrez-Arellano and Mulligan 2018), and therefore on potential pollination supply. However, the increase of forest-cropland edge can enhance pollination to cropland (realised pollination) due to the proximity between crops and natural habitat. Therefore, the relationship between current forest fragmentation and future changes in potential and realised pollination change was assessed.

In order to assess this relationship, first, the current forest cover map (Fig. 4.6a) was vectorized considering all pixels with remaining forest cover ≥50% (Fig. 4.6b). Second, the total perimeter and total area were calculated for this vector forest map (Fig. 4.6c). Third, a fragmentation index was calculated per site by dividing the total perimeter of forest patches (km) by total forest area (km^2). The fragmentation value (km/km^2 or 1/km) per site was plotted against the pollination change per unit of forest lost for both potential (ΔPP/ΔFC) and realised pollination service (ΔRP/ΔFC).

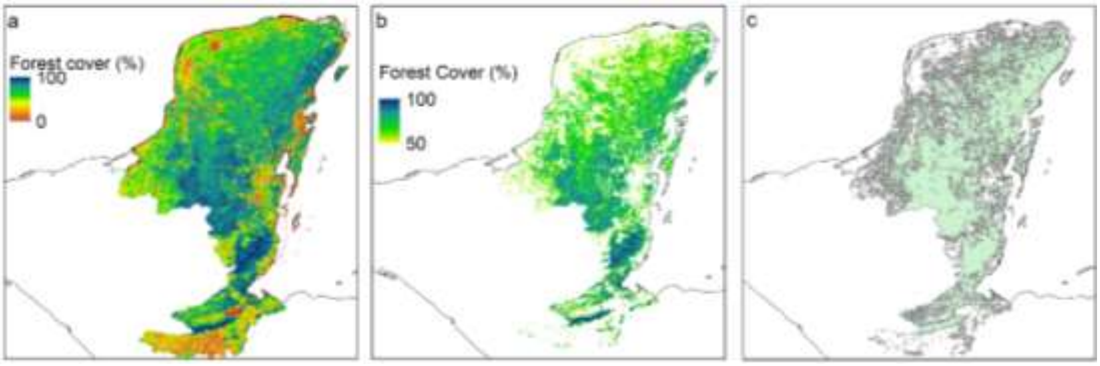


Figure 4.6. Fragmentation measure, Yucatan example. From (a) the current percentage of forest cover map, the areas with a (b) forest cover ≥50% were vectorized to get (c) polygons of forest patches to calculate total area and perimeter per site.

4.2.5. Quantification of change at pantropical scales

To quantify the effects of pollination provision at the pantropical scale, a similar procedure to the regional scale quantification was carried out. However, due to computing time and power limitations, the QUICKLUC model was run at a 10 km resolution. At a global scale, lower deforestation fraction values than the ones used for regional-scale models were set, aiming to capture similar deforestation patterns at both scales.

The model projects deforestation in a pixel only if at least 10% of the forest cover could be lost under the conditions set by the other parameters (see section 4.2.2). In this case, assuming BAU conditions (i.e. constant deforestation rates) at a 10 km resolution, no pixel with forest loss greater than 10% was identified. When a 10% threshold was first used, the outcome maps showed no difference from the baseline forest cover map, i.e. no 10k-resolution pixel had forest cover loss greater to 10% neither in the short nor in the long term. Thus, the selected deforestation thresholds had to be set below 10% to identify the occurrence of deforestation at this coarse resolution. Since the resolution increased tenfold (from 1 km to 10 km), the percentage of fractional deforestation projected forward was proportionately decreased (from 10% to 1%). Therefore, 10%, 50% and 70% deforestation per pixel were projected forward at 1 km resolution, whilst 1%, 5% and 7% were projected forward at 10 km resolution (Fig. 4.7).

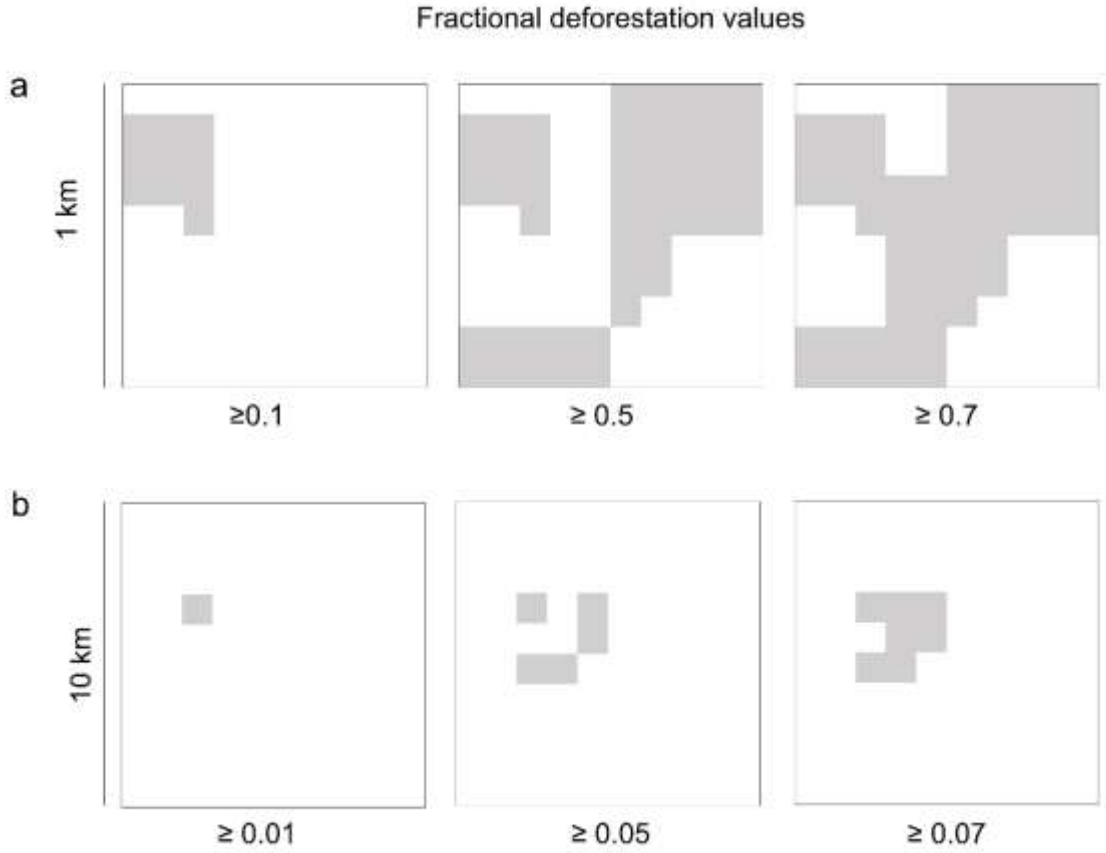


Figure 4.7. Fractional values to project deforestation. The fractional values used at a) 1 km-resolution projected deforestation (grey) in those pixels with a forest cover loss ≥10%, ≥50% and ≥70%, whilst at b)10 km- resolution the values projected deforestation in those pixels with forest cover loss ≥1%, ≥5% and ≥7%, because no deforestation >10% was identified for none of the simulated years (2050 and 2218). This allowed projecting deforestation at a coarser resolution.

The study area was divided using a 5-degree latitude/longitude grid (Fig. 4.8). The pollination provision values within each square were summed and divided by their respective area, obtaining a mean value per square. These mean values were used to calculate the grand mean of the study area, which in turn was used to calculate the change in pollination through time and change per unit of forest lost pantropically. This change was calculated only in those squares where a change in forest cover was projected, due to the mathematical impossibility of dividing the change in pollination service by zero.

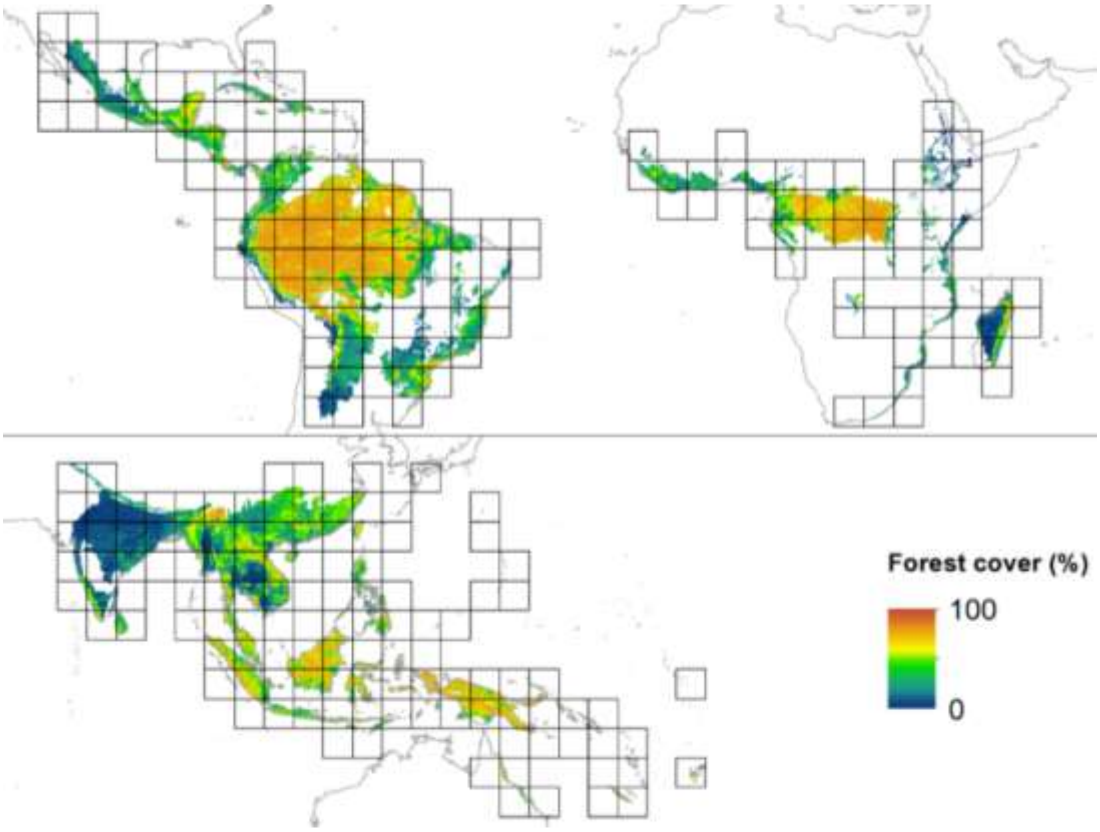


Figure 4.8. Distribution of tropical and subtropical forest of the world (NC 2012) and percentage of forest cover (Hansen et al. 2013). The study area was gridded (5x5 degrees) to calculate the effect of LUCC on pollination provision per square.

An adjustment was made to assess realised pollination at this scale. Realised pollination was defined by restricting foraging sites to the distribution areas of crops highly dependent on pollination plus a 1500 m outside buffer (section 3.2.1.2, Realised pollination). After carrying out the calculations including all values, it was noticed that the estimation of change was obscured by the exceedingly high number of pixels with almost null service value within cropland areas (outside the normal travel radius for forest-dwelling insects). Therefore, to exclude the pixel values outside the mobility range of pollination from natural habitats, instead of a 1500 m outside buffer, a 1500 m ring buffer (i.e. 1500 m outwards and 1500 m inwards) was applied around the cropland edges. The values within this buffer were summed and divided by their respective buffer area, obtaining a mean value per square. Finally, as done for potential pollination, the mean values were used to compare change between baseline and future scenarios.

Fragmentation was estimated per square in the same manner as for regional scale and plotted against the pollination change per unit of forest lost per square. The squares with forest cover ≥50% were treated as forest patches in the fragmentation analysis.

Finally, a linear regression was performed using the mean change in pollination service per unit of forest loss as the dependent variable and baseline fragmentation index as the independent variable. This relationship could indicate that a larger perimeter increases the contact between forest and cropland, therefore increases the probability of pollination by wild bees to crops.

4.3. Results

4.3.1. Projected deforestation and cropland expansion

Four maps of projected deforestation were generated for each site and the tropics. They correspond to the conservation and non-conservation scenarios in the short and long terms (Fig. 4.9). These maps show where deforestation was projected above the 10%, 50% and 70% thresholds in the area of interest and where the nesting suitability (N_j) and floral resources (F_j) were modified according to Table 4.3.

The model allocated deforestation based only on the geographic rules described above, showing physical patterns of change without considering economic or technological changes. Among the sites, the greatest deforestation was projected for Paraguay (Fig. 4.9c), followed by the Amazon (Fig. 4.9a), Yucatan (Fig. 4.9e) and Sri Lanka (Fig. 4.9d). The lowest deforestation was projected in Gabon (Fig. 4.9b).

a

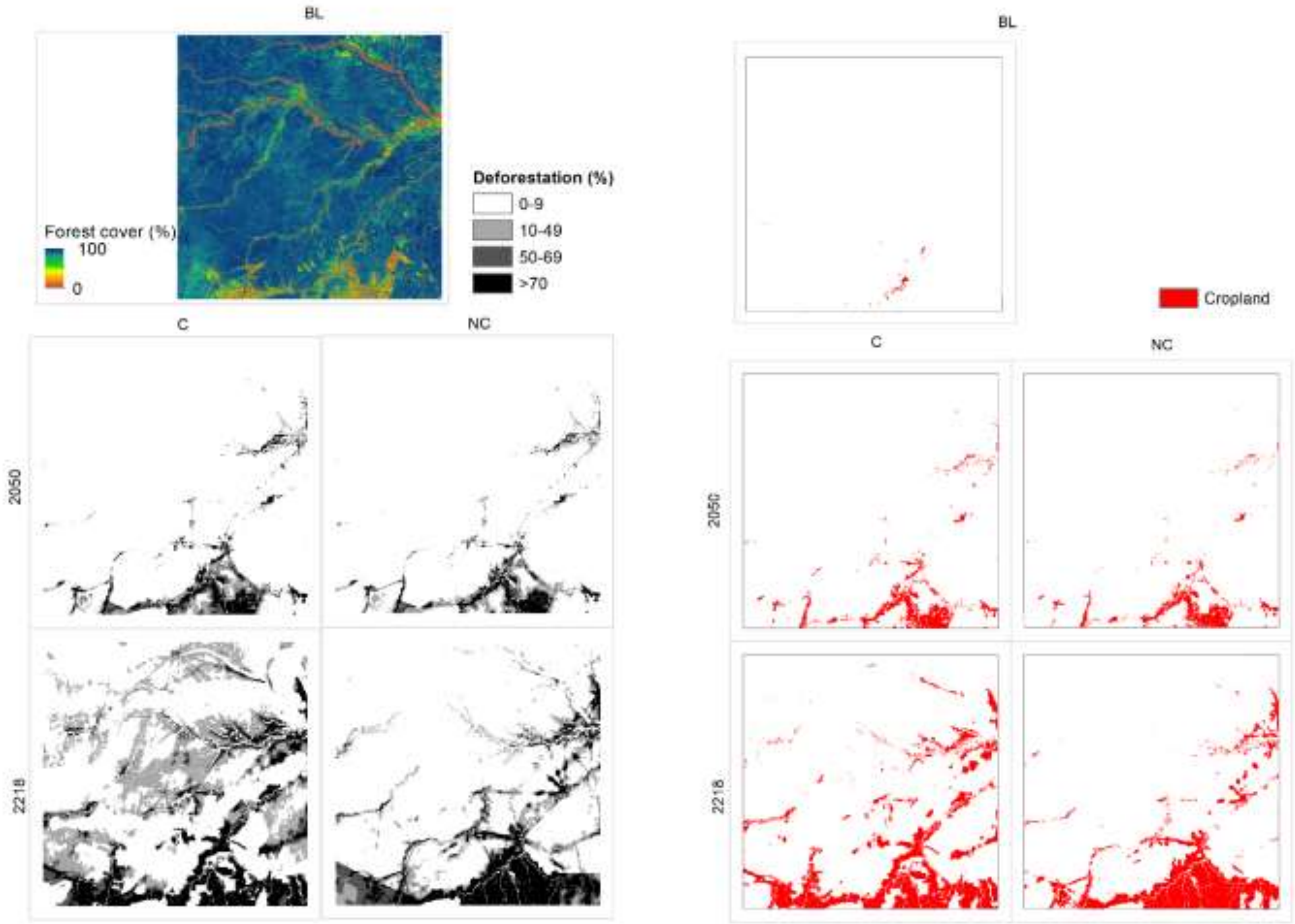


Figure 4.9 Projected deforestation and projected cropland distribution obtained with the QUICKLUC model. Maps correspond to baseline (BL) forest cover (%), projected deforestation (percentage of forest cover loss), and cropland distribution (fractional deforestation, 0.5) for conservation (C) and non-conservation scenarios (NC) by 2050 and 2218 for a) the Amazon, b) Gabon, c) Paraguay, d) Sri Lanka, e) Yucatan and f) tropics.

b

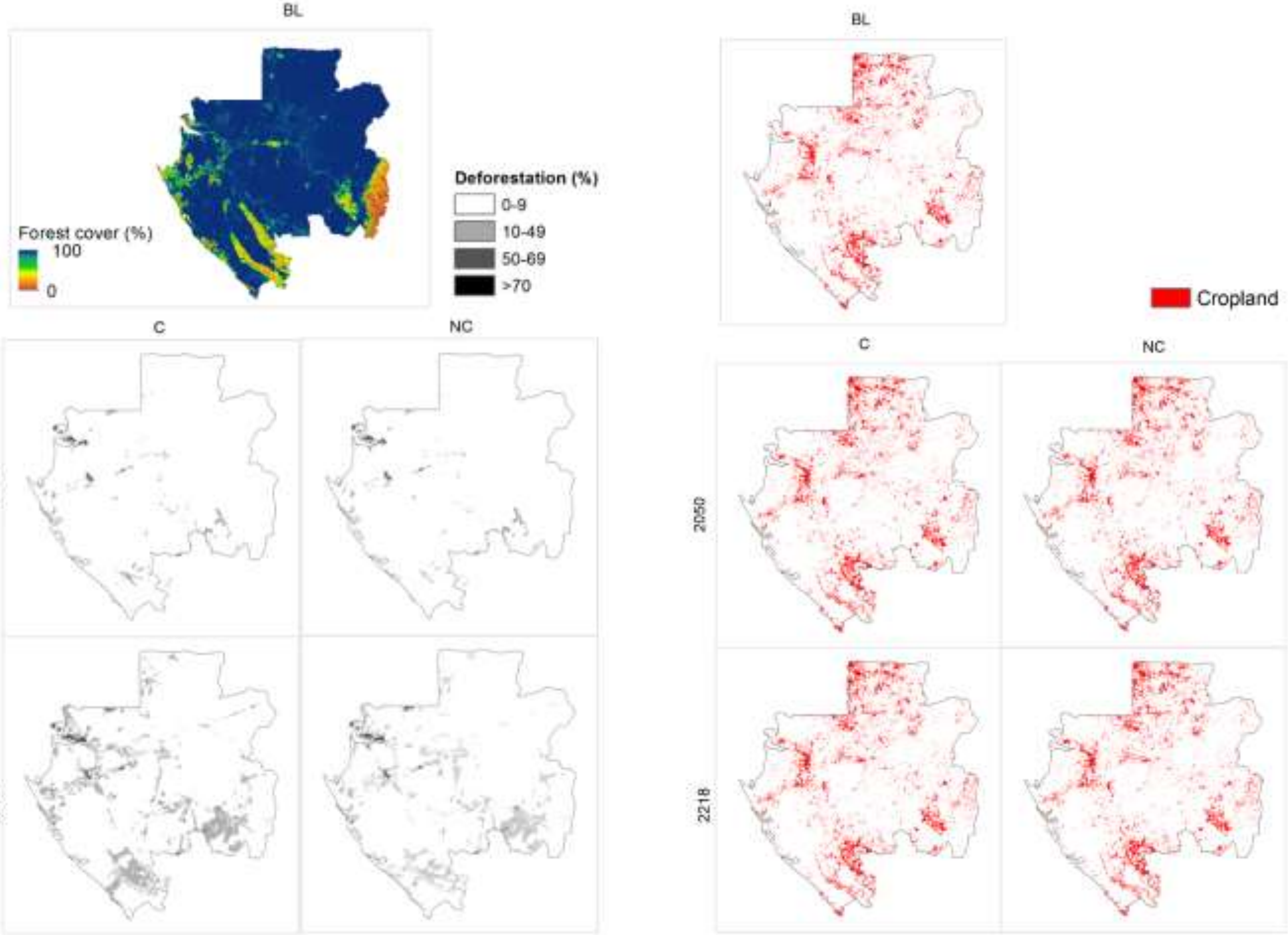


Figure 4.9 Continued. b) Gabon

c

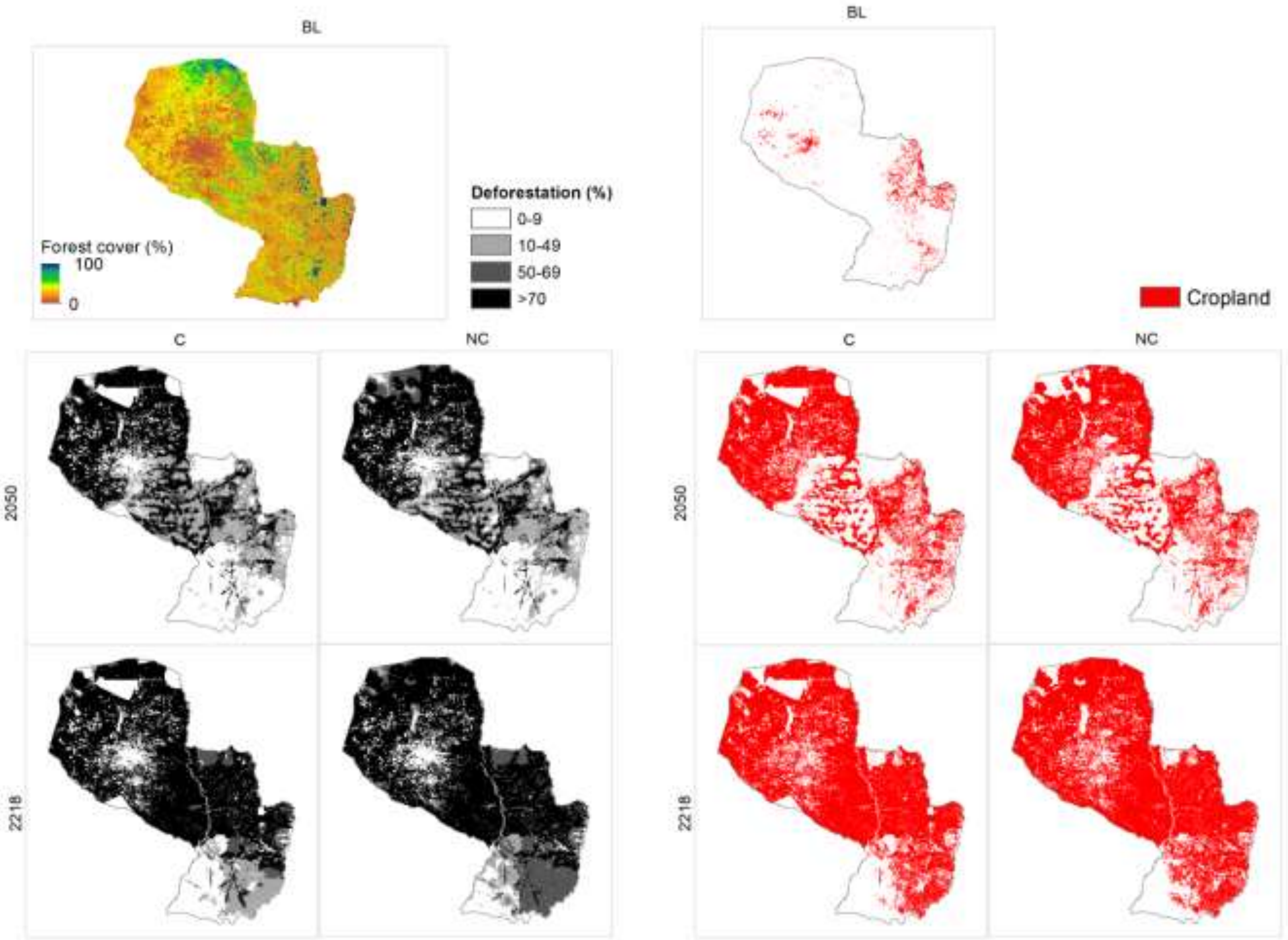


Figure 4.9 Continued. c) Paraguay

d

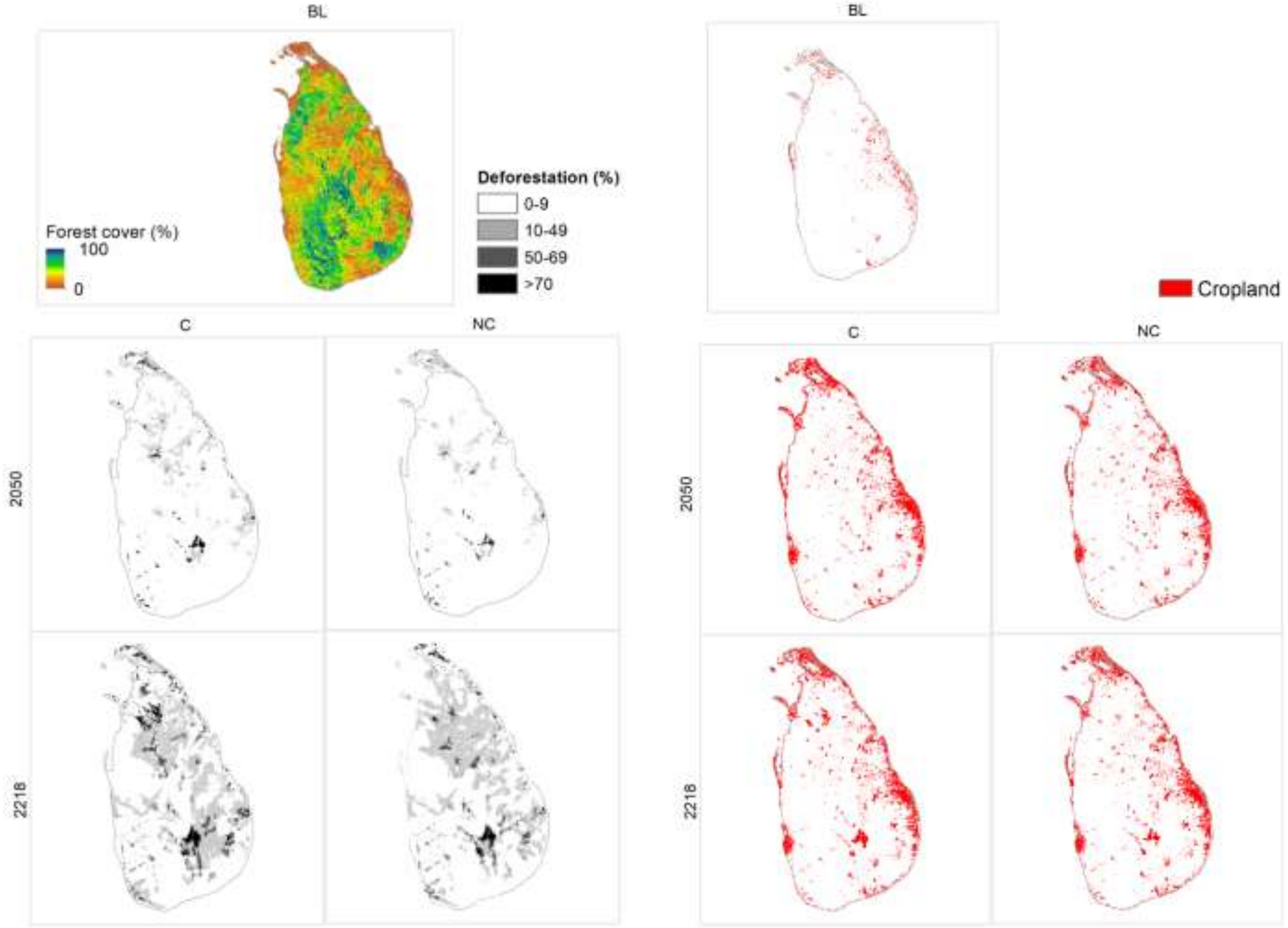


Figure 4.9 Continued. d)Sri Lanka

e

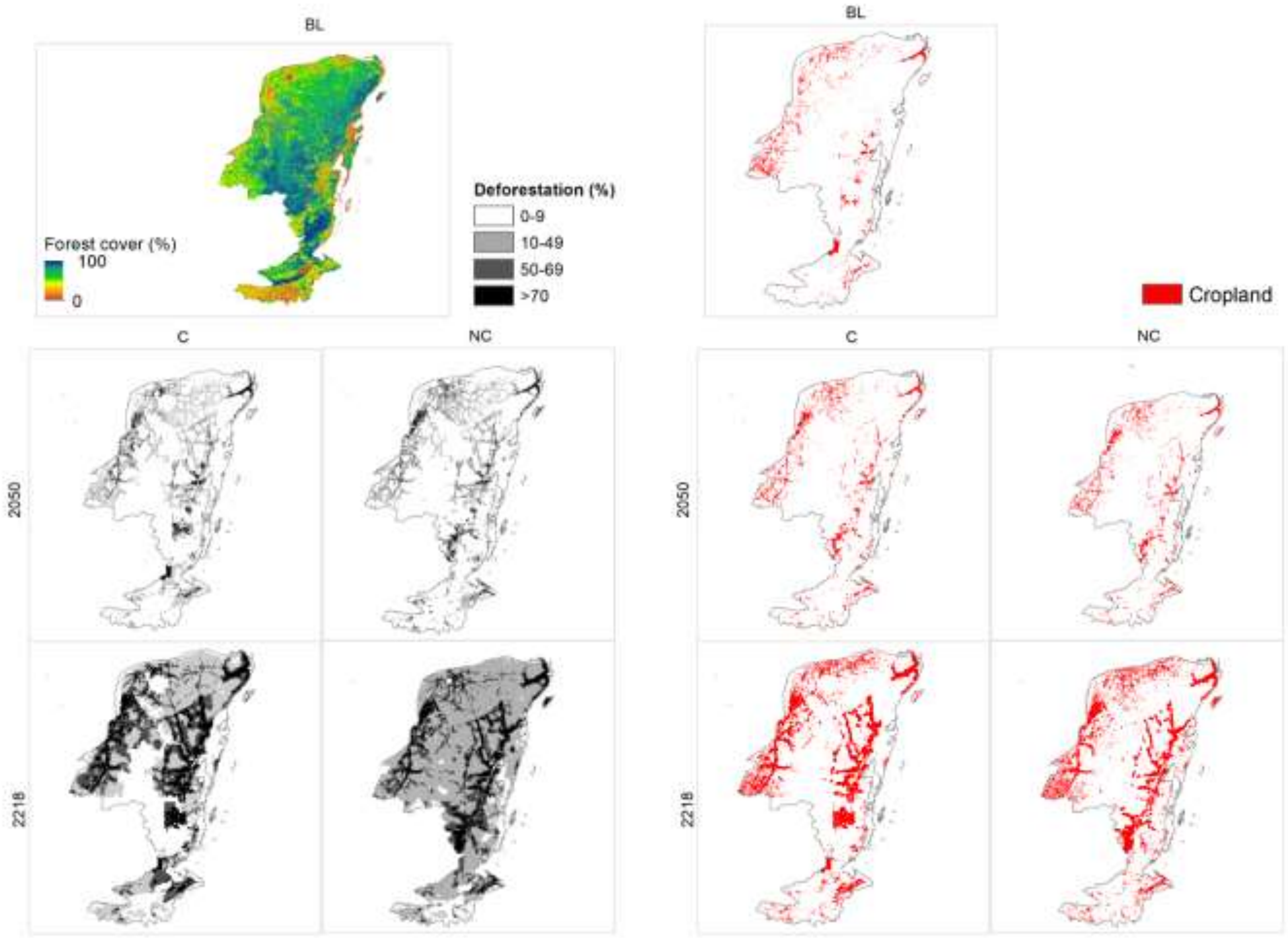


Figure 4.9 Continued. e) Yucatan

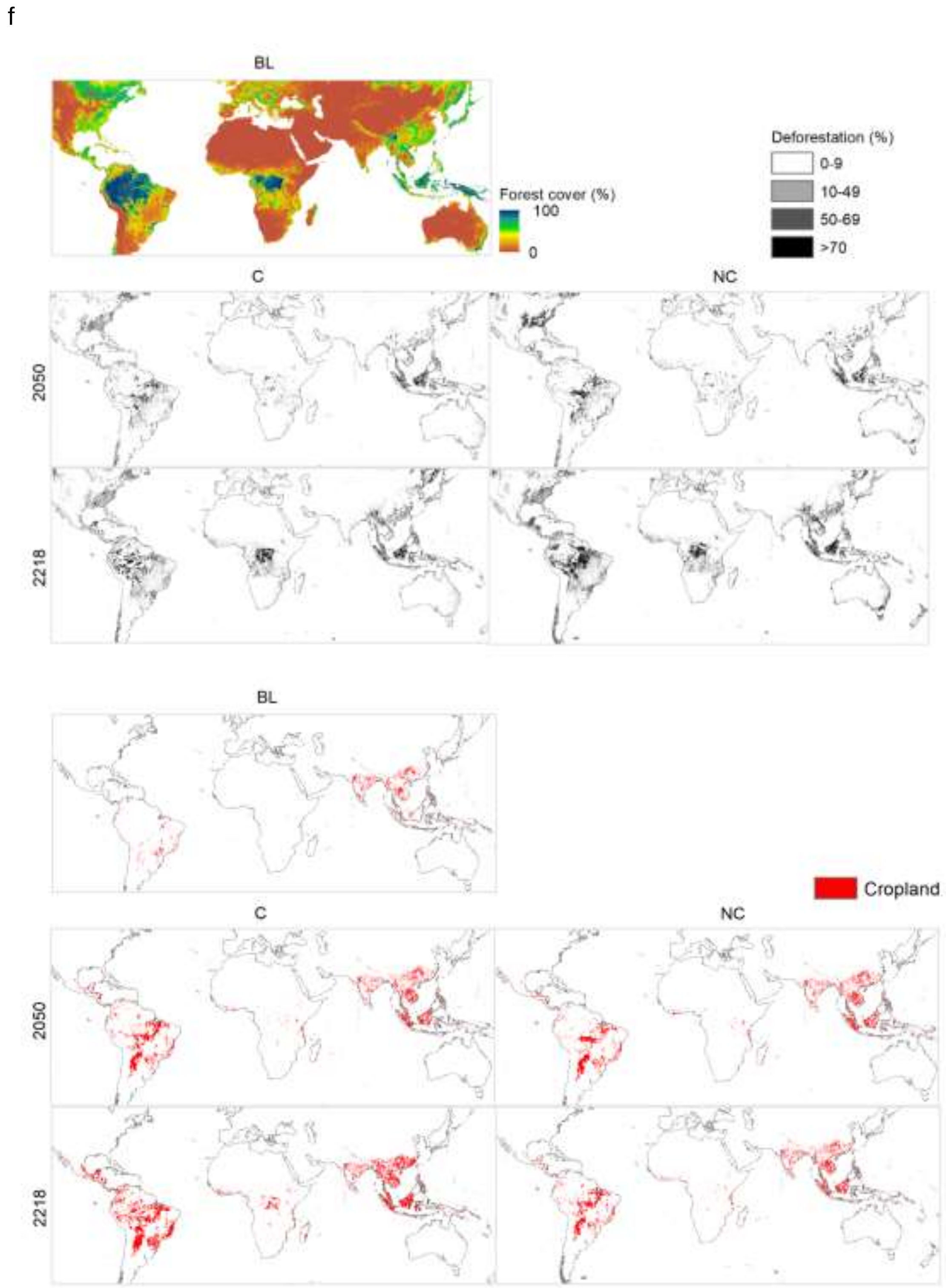


Figure 4.9 Continued. f) tropics

Equally, Figure 4.9 shows the projected distribution of cropland for each scenario and time period. Projected cropland was allocated according to the agricultural suitability of the area (IIASA/FAO 2012). This distribution replaced the distribution of the pollinator-dependent crop (i.e. baseline distribution) used to model realised pollination (section 3.2.1.2).

4.3.2. Regional projected change of pollination service

The effects of agriculturalisation on pollination supply and demand varied among sites through time. The difference among baseline conditions and deforestation rates produced different patterns of distribution of service. In general, a loss of potential pollination is projected for all sites, but for some of the sites realised pollination increased in the short term (Yucatan and Sri Lanka) and for one of them (Yucatan) a gain was also projected in the long term.

This is consistent with the projected proportion of natural habitat-cropland and its effect on pollinator abundance (Fig. 4.10). Since natural habitats are more suitable for wild pollinators (see Table 3.1, and Table 4.3), a higher proportion of natural vegetation tends to produce higher potential and realised service. Landscapes dominated by agricultural land receive little or null service by wild pollinators in areas where suitable habitat is very distant. Thus, the gain or loss of service was greatly determined by the baseline conditions of land cover within and outside protected areas. The results for each site are described in detail below

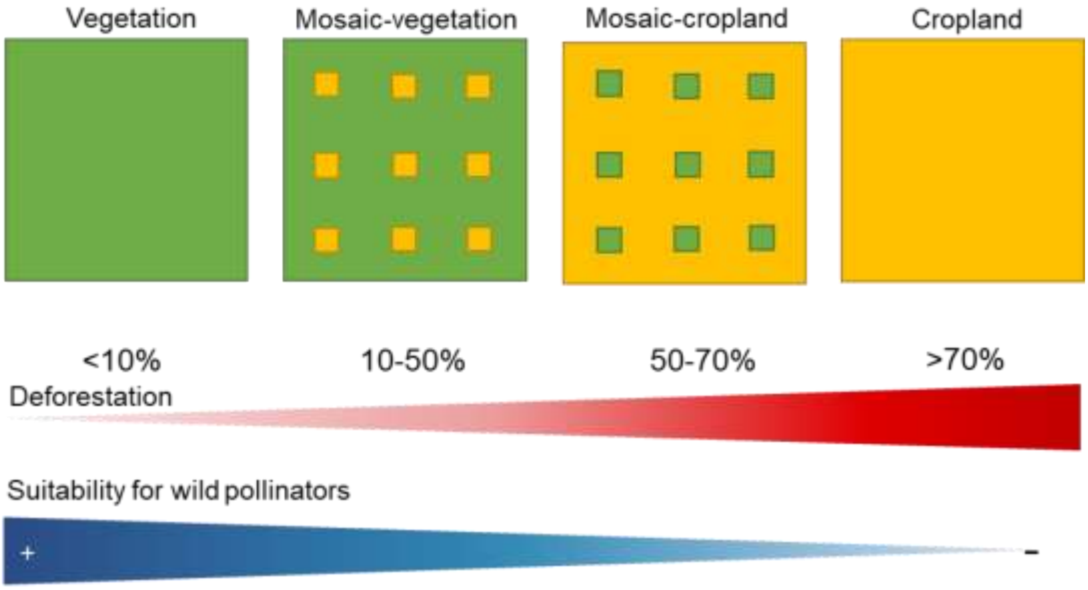


Figure 4.10. Relationship between the proportion of natural habitat-cropland and suitability for wild pollinators. Deforestation increases with agriculturalisation. The higher proportion of natural habitats tends to increase pollination service due to the higher suitability for wild pollinators.

Amazon

A mean of 72.3% forest cover is currently estimated in the Amazon region, the highest baseline forest cover among the assessed sites. A 3.6% forest cover loss is projected by C2050 and a 12.4% loss by C2218; while projected a mean forest cover loss of 1.9% and 9.6% for NC2050 and NC2218 respectively (Fig. 4.11a).

A decrease for mean potential and realised pollination was projected for all scenarios compared to mean baseline pollination (Fig. 4.11b). For potential pollination, the loss is higher in the conservation scenario, especially in the long term, than in non-conservation. Realised pollination shows a significant loss under both scenarios, in the short and long terms, the decrease is greater in non-conservation than in conservation conditions.

Regarding the change of service per unit of forest lost (i.e. the amount of change, loss or gain, in service due to a 1% forest cover loss, Fig. 4.11c), for potential pollination, the proportion of decrease is lower for conservation than for non-conservation by 2050. This condition is inverted by 2218, where the decrease is greater in the conservation scenario, although the difference between scenarios is lower in the long term.

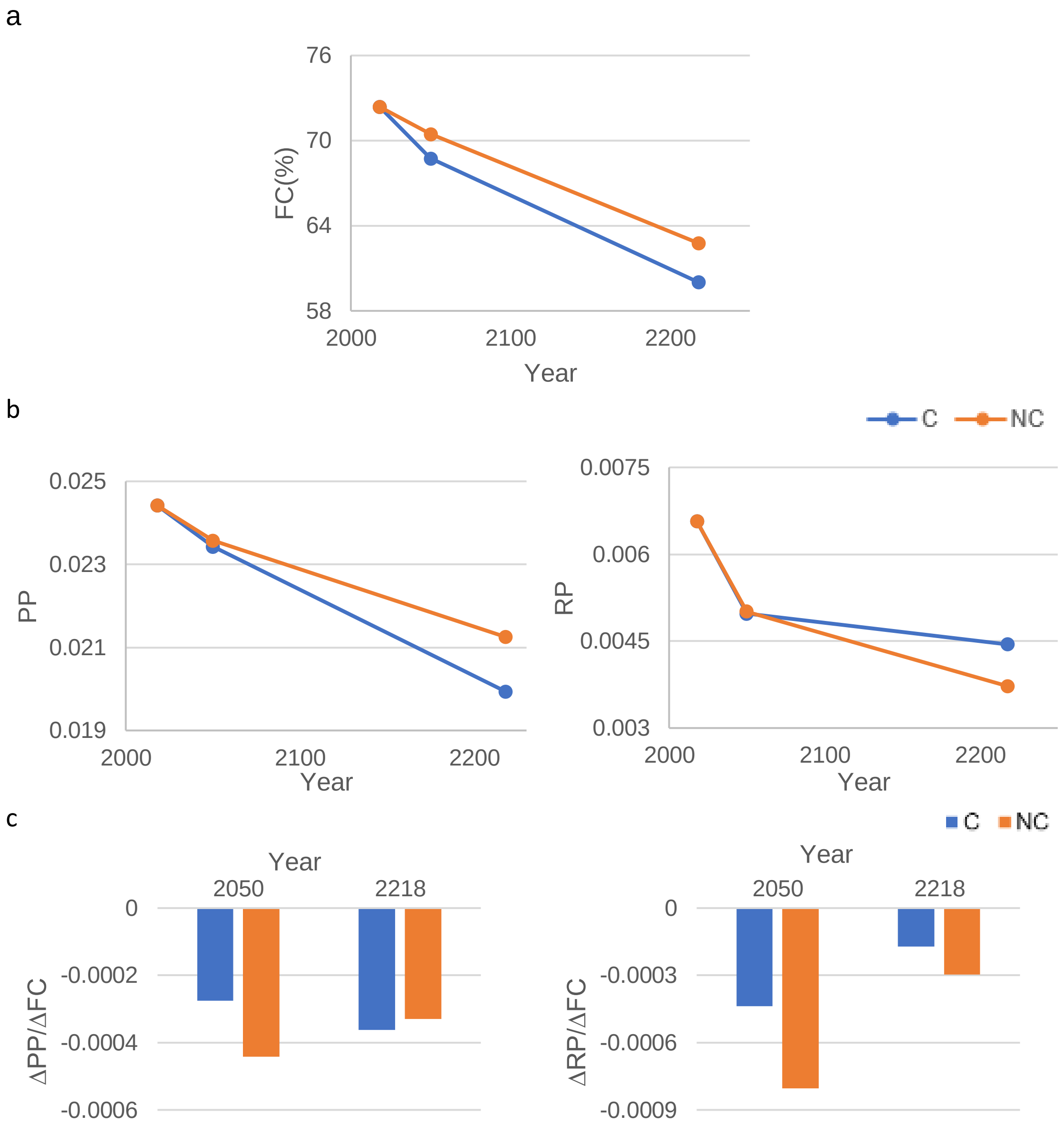


Figure 4.11. Amazon’s change in pollination service. a) Forest cover, b) mean potential (PP) and mean realised pollination (RP) and c) change in mean potential (ΔPP) and mean realised (ΔRP) pollination per unit of forest cover loss (ΔFC) for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

While on average a loss of potential pollination is projected, the variation of values increased considerably through time and throughout the region for both scenarios (Fig. 4.12). The occurrence of extreme values (outliers), both maximum and minimum, increased compared to baseline distribution. While some areas decreased their value, others increased them, being more evident by 2218. In the long term, under conservation conditions, the change in value is spread throughout the region, whilst for non-conservation, the loss is mostly concentrated at the south of the study area, where cropland is currently distributed (Fig. 4.5).

Regarding realised pollination values (Fig. 4.13), as the occurrence of cropland increases most of the pixels present lower values compared to baseline distribution. However, some pixels considerably increased their values compared to current conditions. These are mainly distributed in the edges of cropland patches where proximity of new cropland to remaining forest increases service provision.

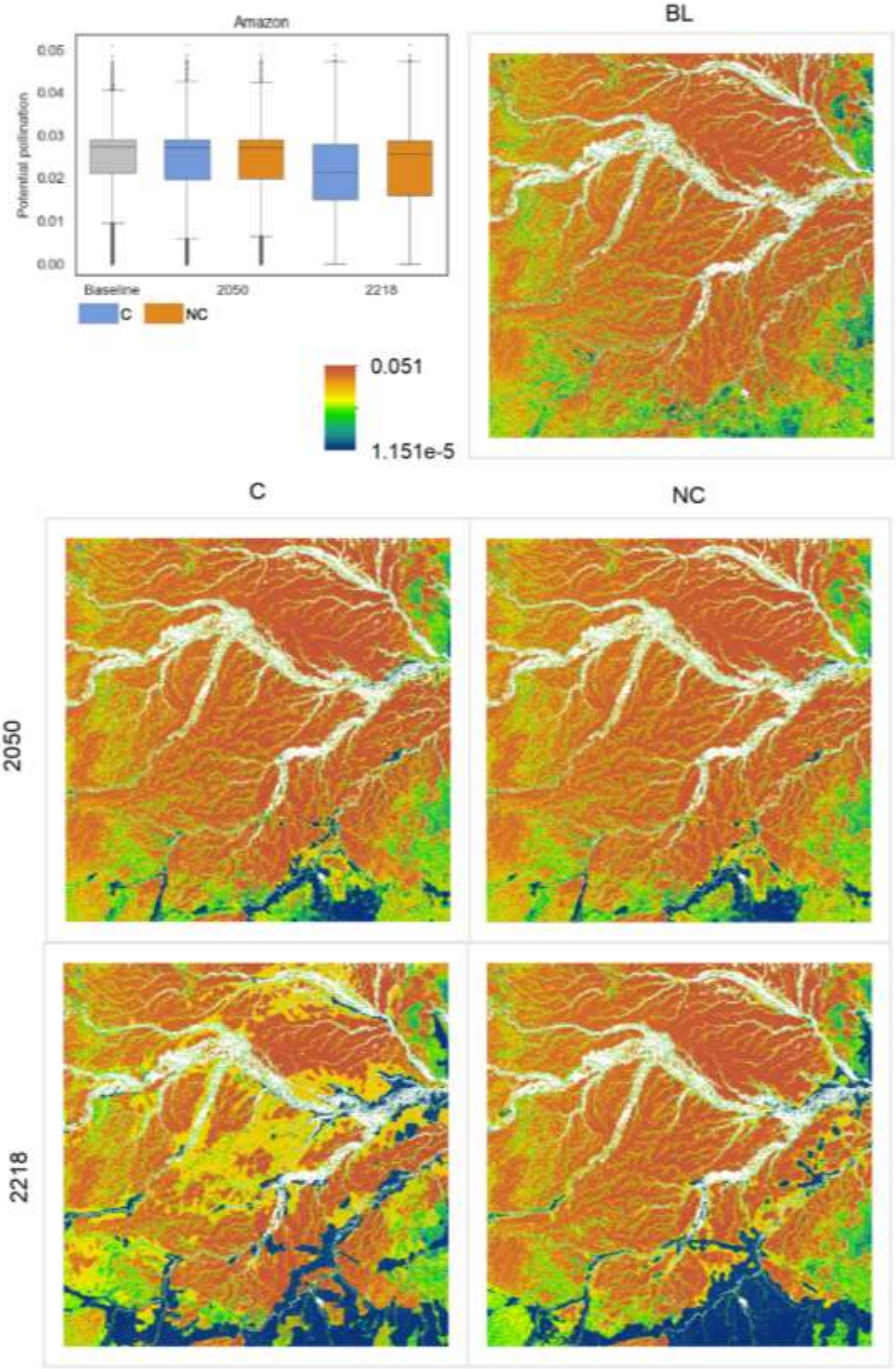


Figure 4.12. Amazon's projected potential pollination. Boxplot shows the distribution of potential pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

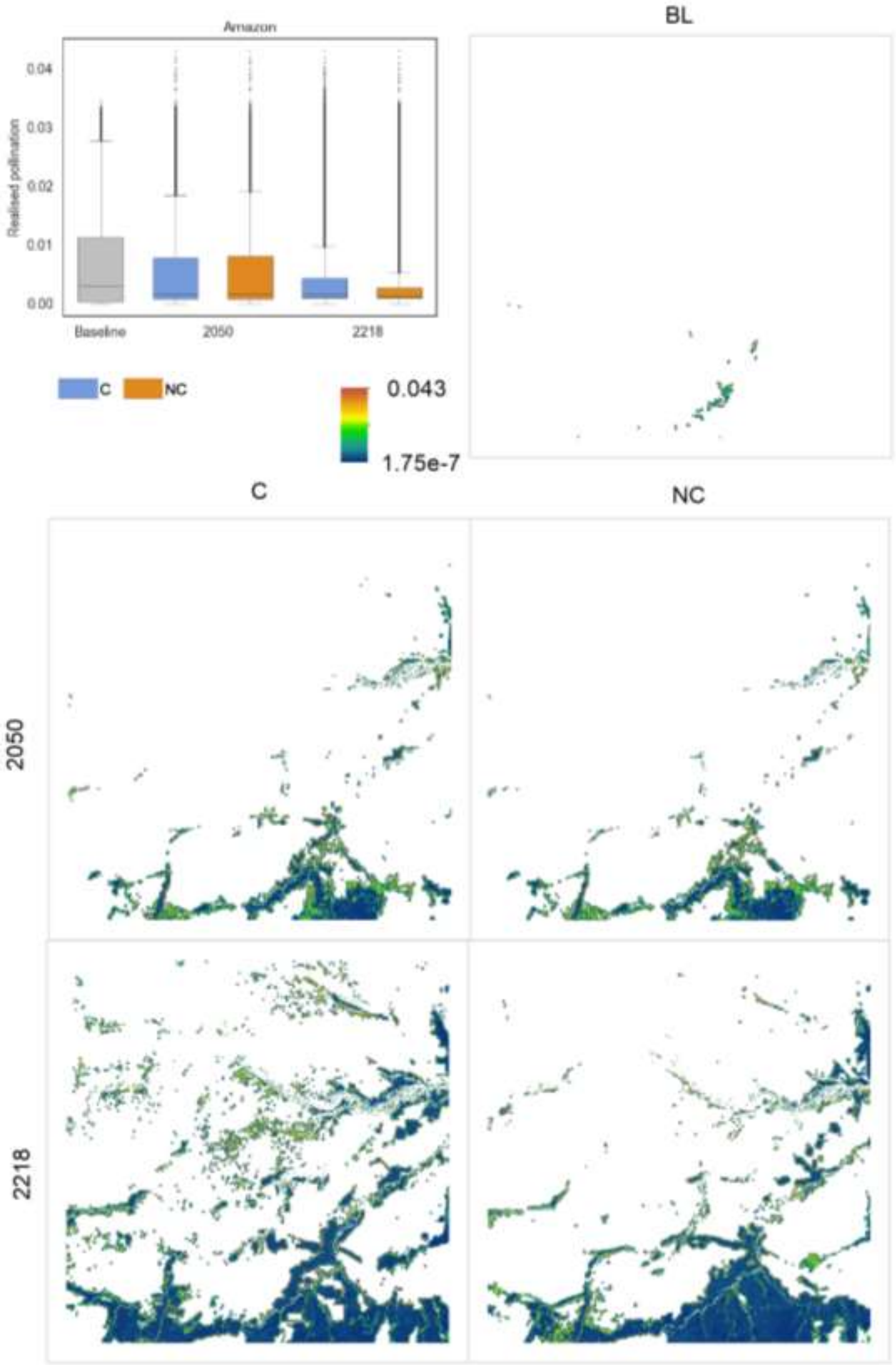


Figure 4.13. Amazon's projected realised pollination. Boxplot shows the distribution of realised pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

Gabon

A mean of 39.9% forest cover is estimated currently in Gabon and less than 1% forest cover loss is projected in the short and long terms. The loss was lower under the conservation scenario in the short and long terms: C2050, −0.19%; NC2050, −0.21%; C2218, −0.22%; NC2218, −0.24% (Fig. 4.14a).

A decrease in potential and realised pollination was projected for both scenarios (Fig. 4.14b), and the mean loss was greater in the conservation scenario.

Considering the change of service per unit of forest lost, the change is greater for potential and realised pollination in conservation scenario. This relationship remains through time (Fig. 4.14c).

In general, excluding outlier values (see Fig. 4.15 Boxplot) of the potential pollination distribution, there is a continuous decrease throughout the region and occurs equally for both scenarios (Fig. 4.15). A decrease was also present for realised pollination. However, a greater decrease occurred under a conservation scenario by 2218 (Fig. 4.16).

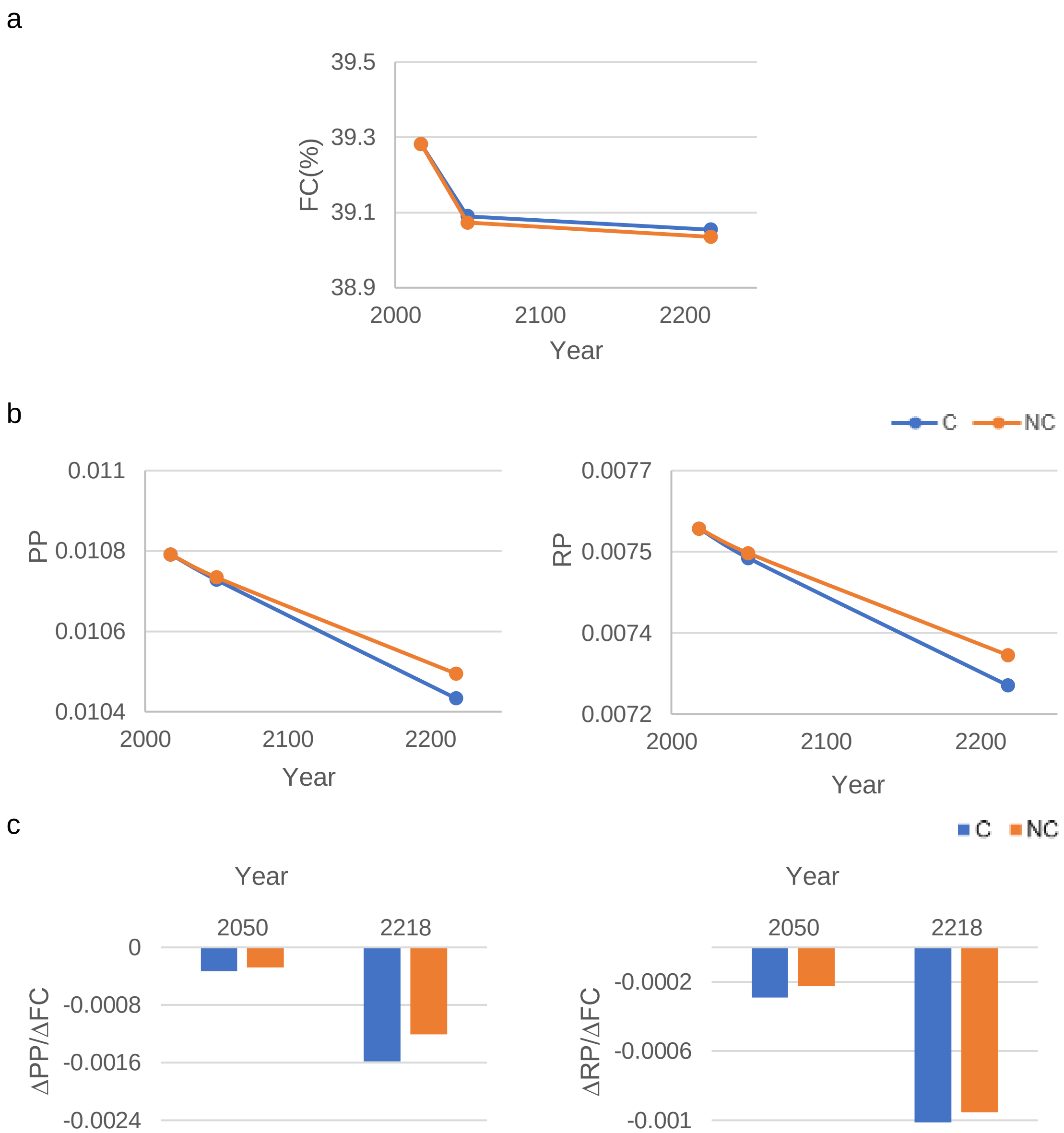


Figure 4.14. Gabon's change in pollination service. a) Forest cover, b) mean potential (PP) and mean realised pollination (RP) and c) change in mean potential (ΔPP) and mean realised (ΔRP) pollination per unit of forest cover loss (ΔFC) for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

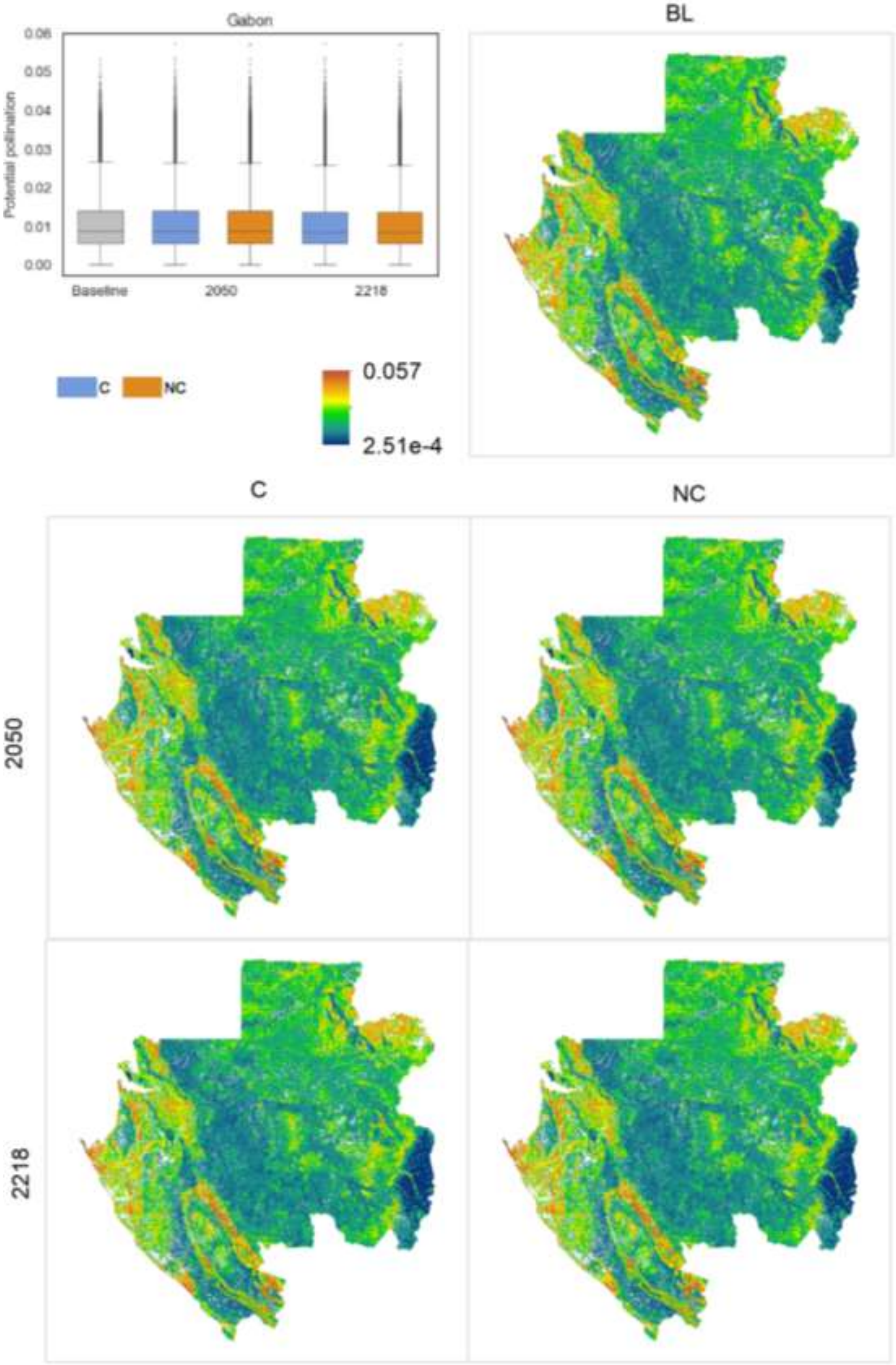


Figure 4.15. Gabon's projected potential pollination. Boxplot shows the distribution of potential pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

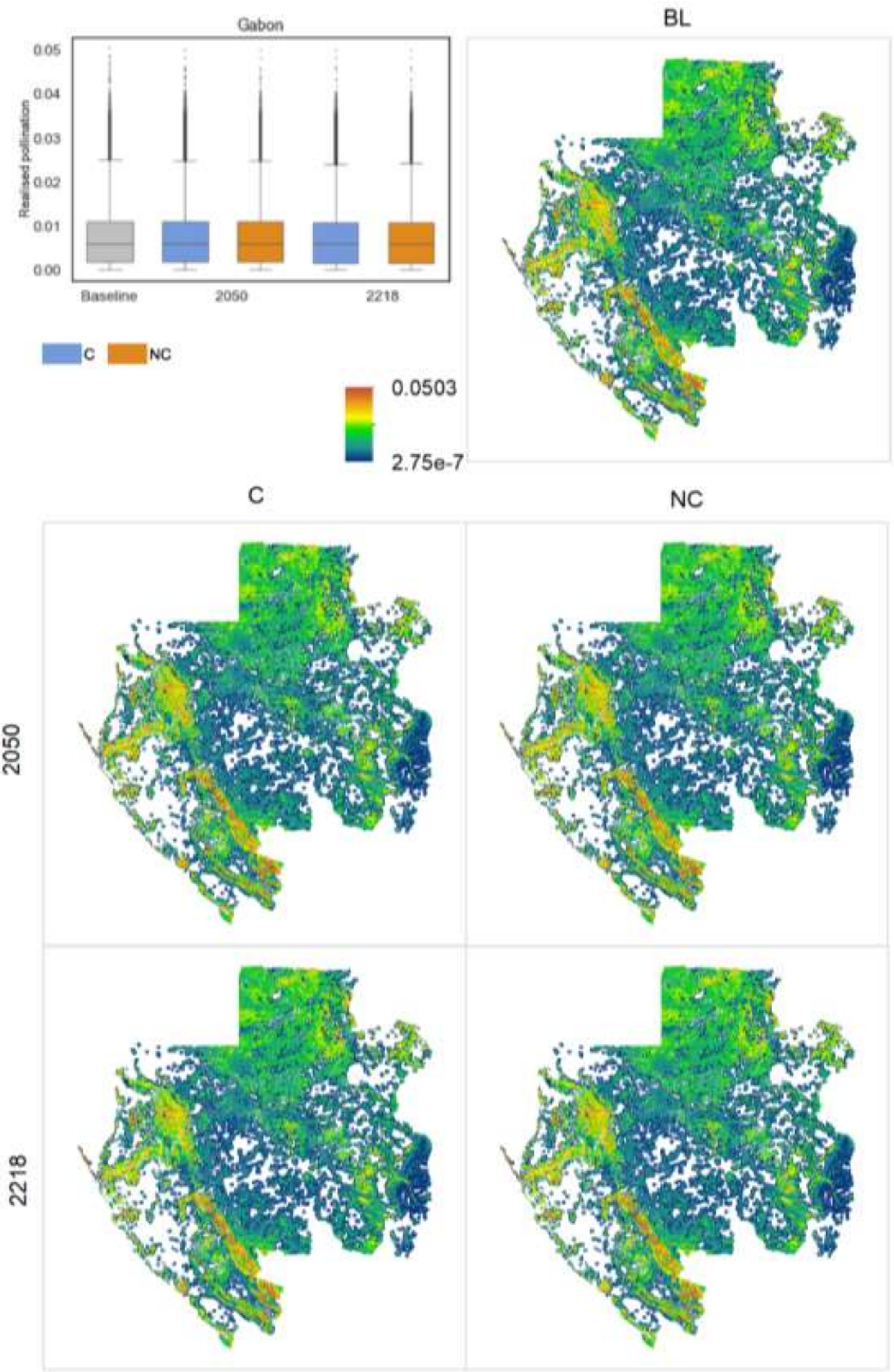


Figure 4.16. Gabon's projected realised pollination. Boxplot shows the distribution of realised pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

Paraguay

Paraguay is currently the least forested among the assessed sites with a 24.2% mean forest cover. Deforestation projections suggested a reduction of more than a half of the current cover in the short term, a mean of 11.5% mean forest cover for the conservation scenario and 10.5% for the non-conservation scenario was projected. By 2218, it was projected a 6.1% and 4.7% mean forest cover respectively (Fig. 4.17a).

The decrease in potential pollination by 2050 is similar under both scenarios but by 2218 the difference between scenarios increases. The non-conservation scenario presented the lowest service supply. In contrast, for realised pollination, the difference between scenarios is greater in the short term than long term (Fig. 4.17b).

The change on potential and realised pollination per unit of forest cover loss was higher in a conservation scenario in both time periods. For potential pollination, this proportion was higher by 2050 than by 2218. In contrast, for realised pollination, the proportion was higher by 2218 than in 2050 (Fig. 4.17c).

A considerable decrease in potential pollination values occurred in the short term and continued in the long term, especially in the central region of the country (Fig. 4.18). The conservation scenario kept the highest values for potential pollination, mostly concentrated in current protected areas.

Regarding realised pollination, there was a general decrease in the country, except for the edges of remnant natural vegetation and riversides (corridors). The C2218 presented the highest maximum values for the region, as shown by the outlier values in the boxplot of Fig. 4.19.

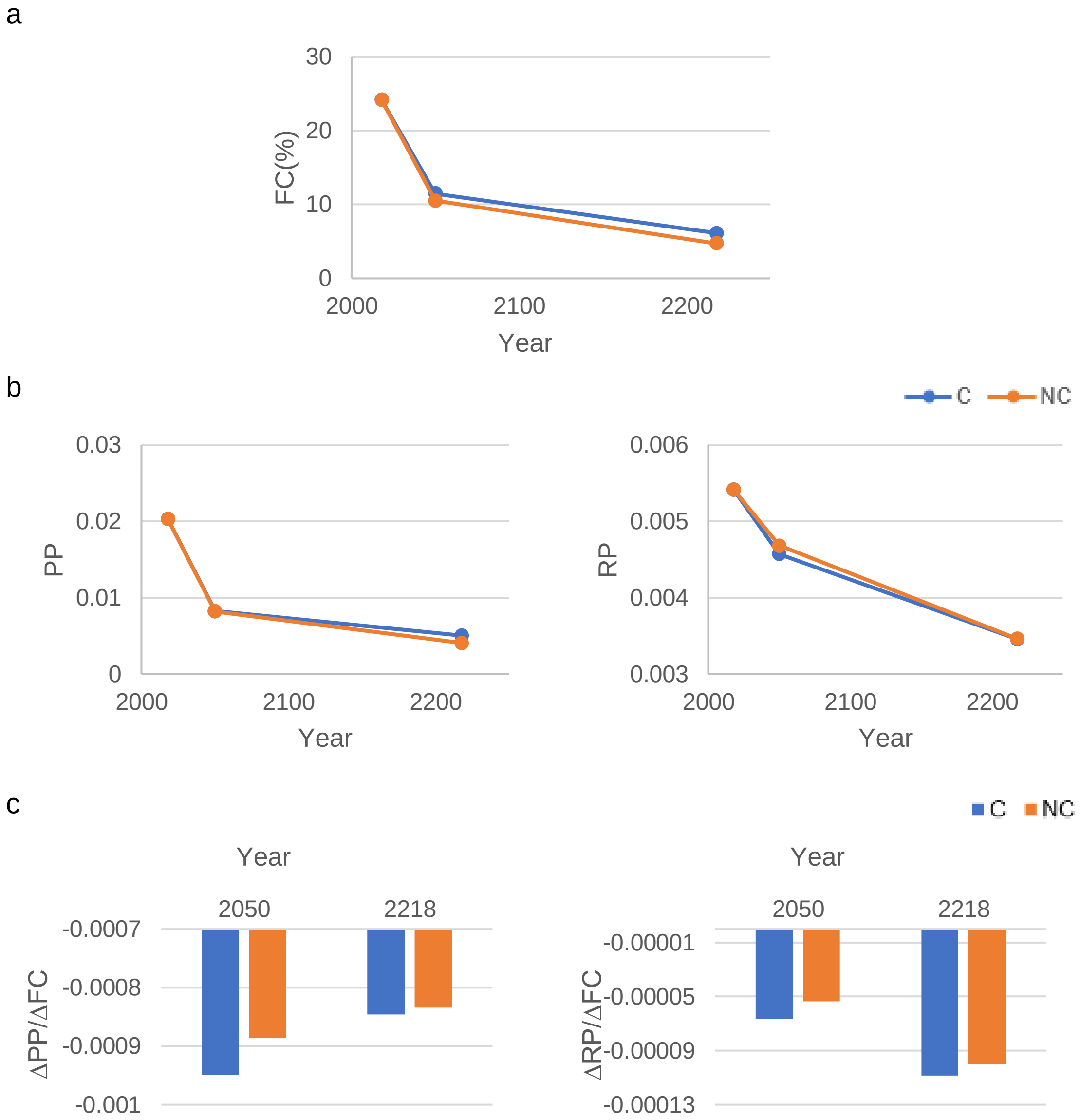


Figure 4.17. Paraguay's change in pollination service. a) Forest cover, b) mean potential (PP) and mean realised pollination (RP) and c) change in mean potential (ΔPP) and mean realised (ΔRP) pollination per unit of forest cover loss (ΔFC) for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

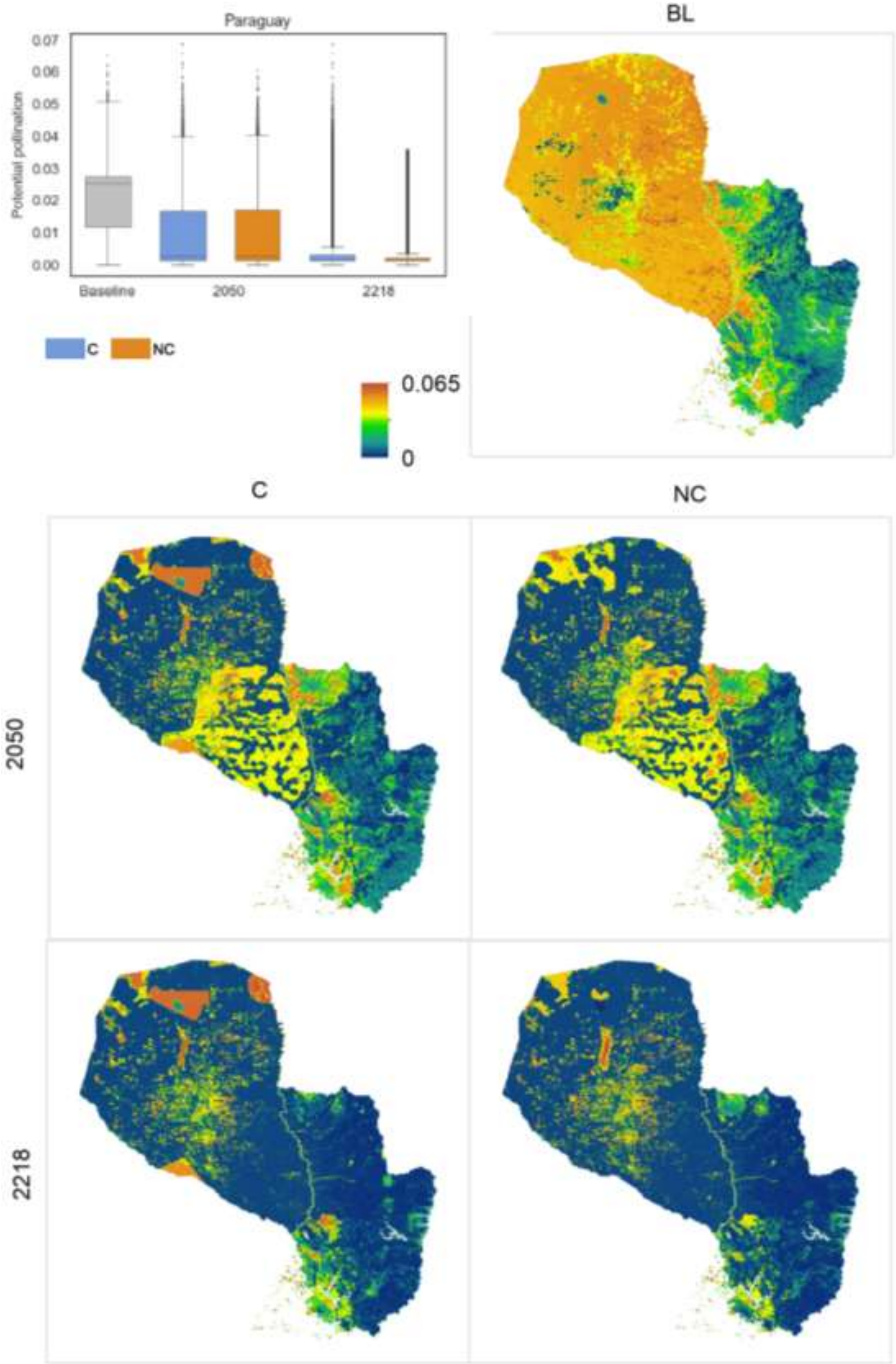


Figure 4.18. Paraguay's projected potential pollination. Boxplot shows the distribution of potential pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

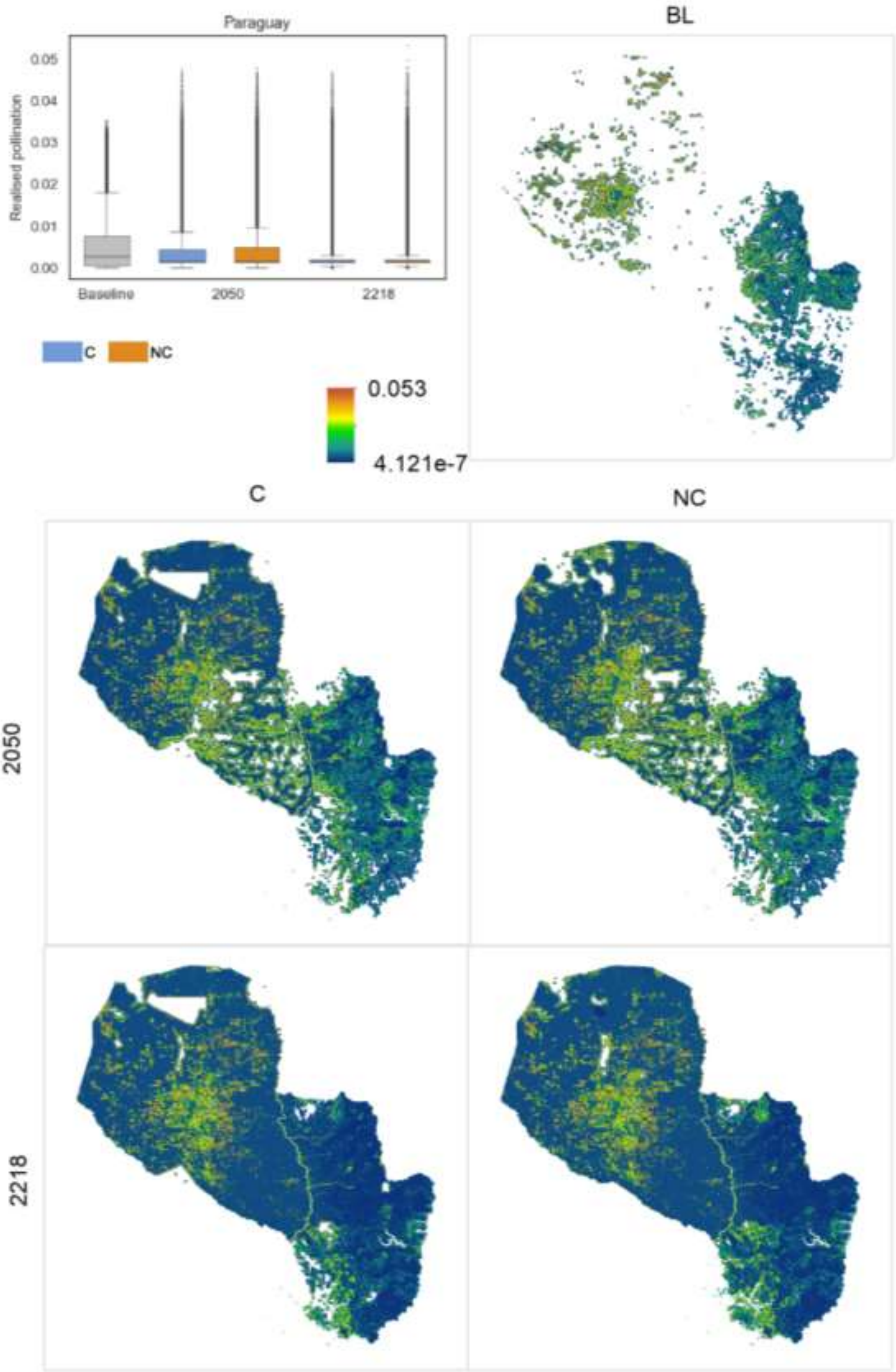


Figure 4.19. Paraguay’s projected realised pollination. Boxplot shows the distribution of realised pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

Sri Lanka

Currently, an average of 32.3% forest cover was estimated for Sri Lanka. Under the conservation scenario, a 31.8% mean forest cover was projected by 2050 and 30.2% by 2218. A 31.9% by 2050 and 31.0% by 2218 was projected under non-conservation conditions (Fig. 4.20a).

A greater decrease of potential pollination was projected in a conservation scenario than in non-conservation in the short term. However, NC2218 presented a greater loss in the long term.

Initially, an increase in realised pollination is projected by 2050 for both scenarios. This changes in the long term, a decrease below the baseline was projected for both scenarios, especially in NC2218 (Fig. 4.20b).

In terms of the change in service per unit of forest lost (Fig. 4.20c), for potential pollination, the loss was greater for C2050 than for NC2050. In contrast, by 2218 the proportion of service lost was greater in the non-conservation scenario. For realised pollination, the gain in service in the short term was higher in non-conservation, while in the long term the loss is lower under conservation conditions.

The change in potential pollination is mostly concentrated in the northern part of the island and is more evident in the long term in NC2218 (Fig. 4.21). For realised pollination, the projection of service reached a peak by 2050 under a non-conservation scenario, but in the long term, the realised service decreases and the number of pixels with lower values increased compared to the conservation scenario (Fig. 4.22).

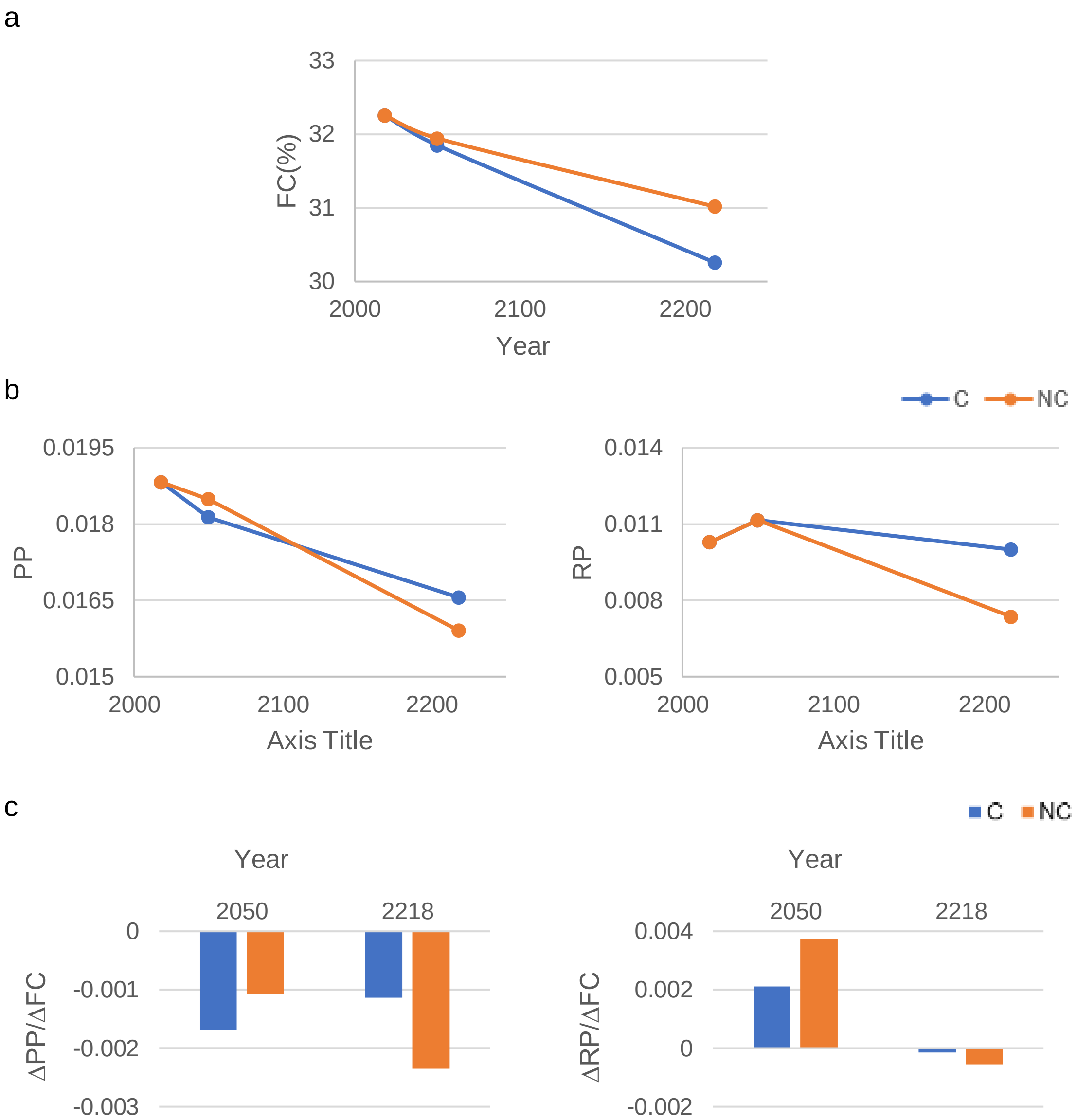


Figure 4.20. Sri Lanka's change in pollination service. a) Forest cover, b) mean potential (PP) and mean realised pollination (RP) and c) change in mean potential (ΔPP) and mean realised (ΔRP) pollination per unit of forest cover loss (ΔFC) for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

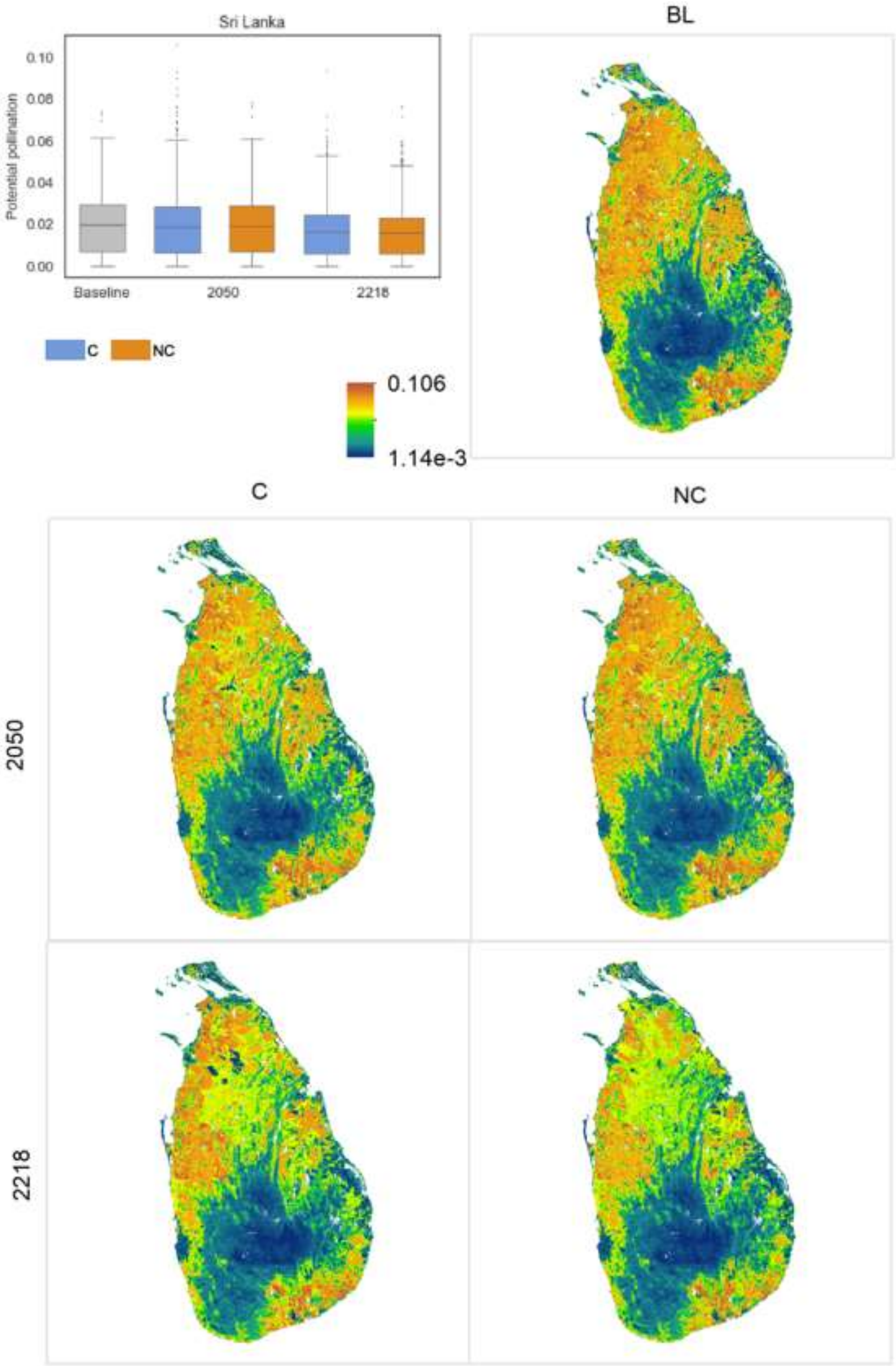


Figure 4.21. Sri Lanka's projected potential pollination. Boxplot shows the distribution of potential pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

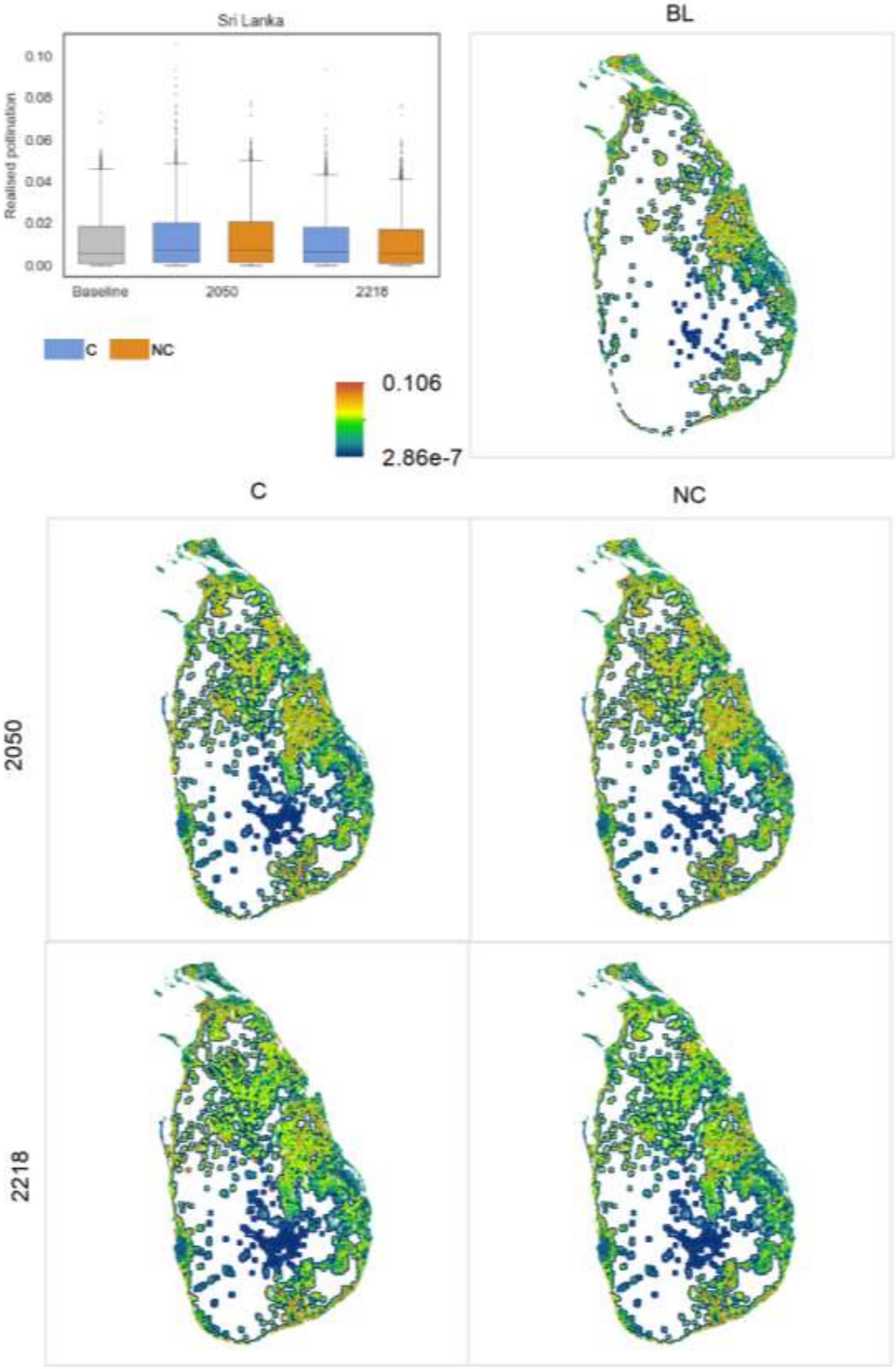


Figure 4.22. Sri Lanka's projected realised pollination. Boxplot shows the distribution of realised pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

Yucatan

The current forest cover estimated for Yucatan was 50.2%, a reduction to 47.3% and 47.9% was projected by 2050 in conservation and non-conservation scenario, respectively. By 2218 the projected forest cover was 31.9% in a conservation scenario and 34.0% in non-conservation (Fig. 4.23a).

A decrease of potential pollination was projected for both scenarios in the short and long-term. In contrast, realised pollination increased by 2050, reaching a peak in a conservation scenario (Fig. 4.23b). Realised pollination continued to be higher in 2218 than the current estimation, especially in a non-conservation scenario, although it decreased compared to 2050.

The change in service per unit of forest loss was negative for potential pollination and was greater under a non-conservation scenario. In contrast, the change was positive for realised pollination and considerably higher in the short-term projections (4.23c).

Potential pollination presented a relatively even decrement in the north-eastern area of the peninsula, but a major loss was concentrated along the coastlines of the Gulf of Mexico and the Caribbean Sea (Fig. 4.24). Realised pollination showed the highest values by C2050, mainly concentrated at the North-west of the region (Fig. 4.25).

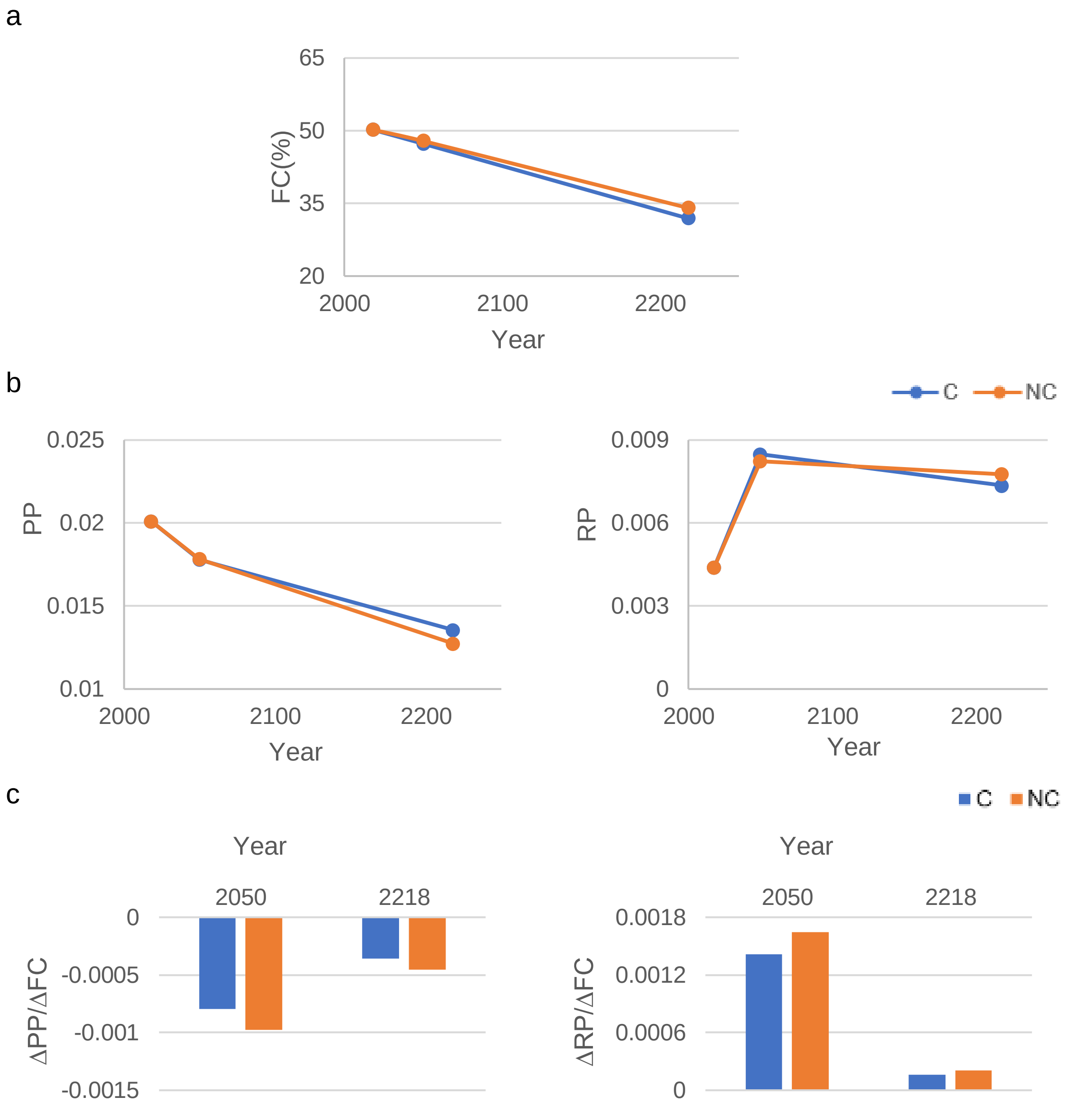


Figure 4.23. Yucatan's change in pollination service. a) Forest cover, b) mean potential (PP) and mean realised pollination (RP) and c) change in mean potential (ΔPP) and mean realised (ΔRP) pollination per unit of forest cover change (ΔFC) for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

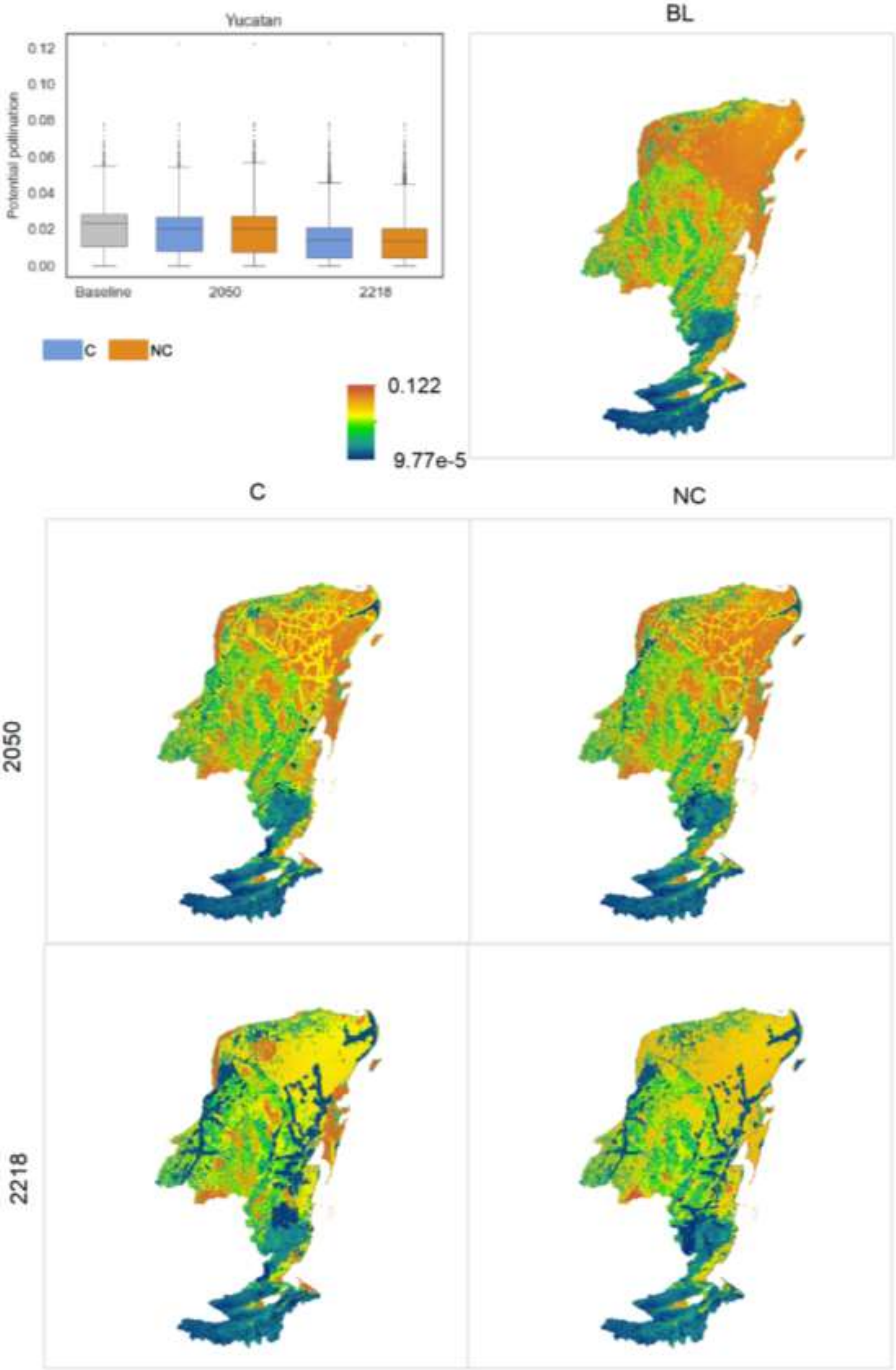


Figure 4.24. Yucatan's projected potential pollination. Boxplot shows the distribution of potential pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

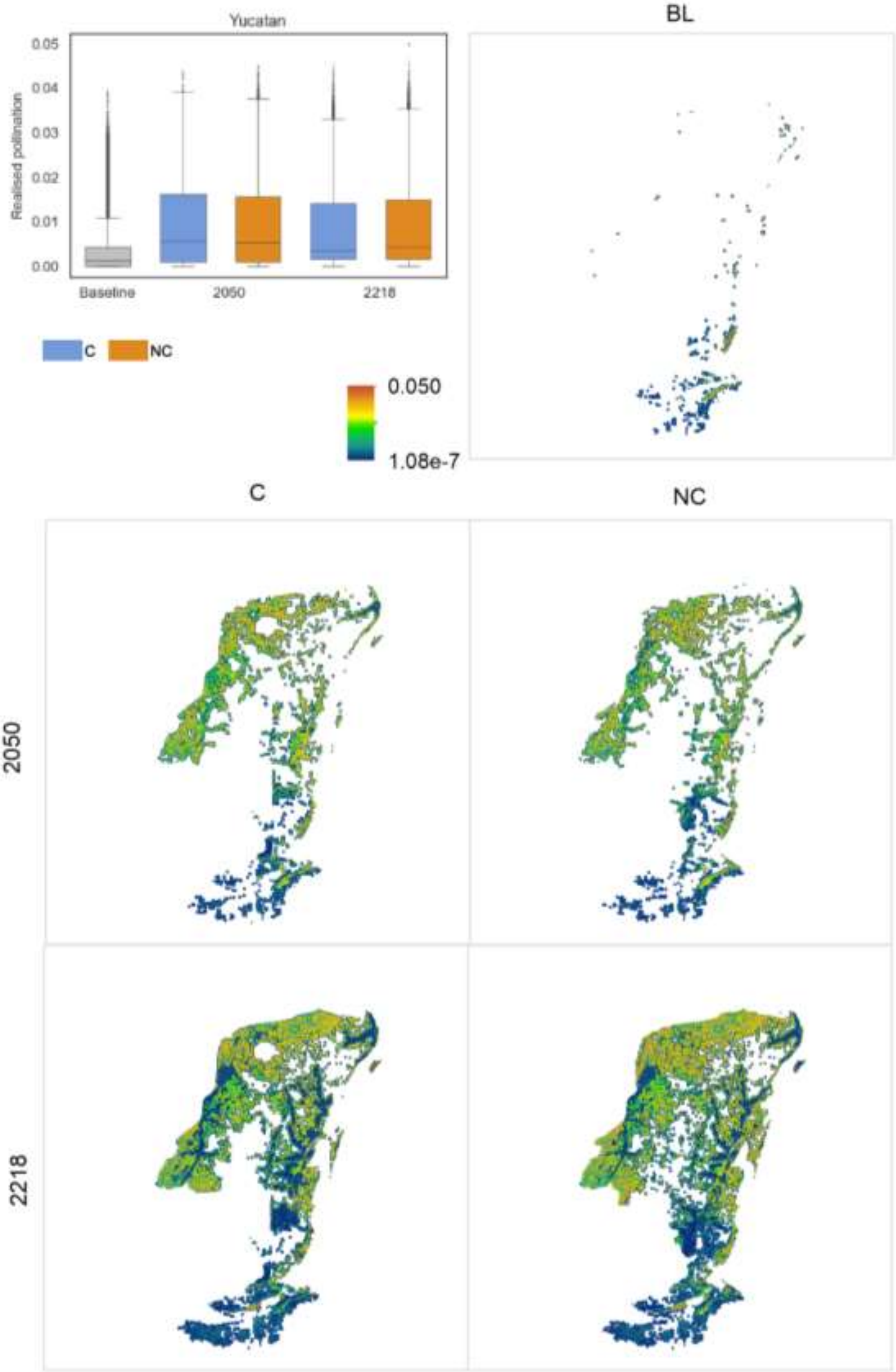


Figure 4.25. Yucatan's projected realised pollination. Boxplot shows the distribution of realised pollination values for the region corresponding to the baseline map (BL) and projected maps for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

Regarding the relationship of service provision with regional baseline fragmentation, the area with the lowest fragmentation was the Amazon (0.14) with a forest cover >50% area of 1,128,297 km^2 and a 156,585 km perimeter, followed by Yucatan (0.59), with 130,222 km^2 and 77,202 km, Gabon (0.83) with 106,303 km^2 and 88,482 km of area and perimeter respectively. The region with the highest fragmentation was Paraguay (1.71) with 31,106 km^2 of forest area and 53,207 km perimeter, followed by Sri Lanka (1.51) with an area of 15,093 km^2 and a perimeter of 22,828 km (Fig. 4.26).

When the projected change in service provision per unit of forest loss per site was plotted against current fragmentation no clear pattern was observed among the sites. The change varied irrespective of the increase in fragmentation and projected deforestation rate (Fig14.27).

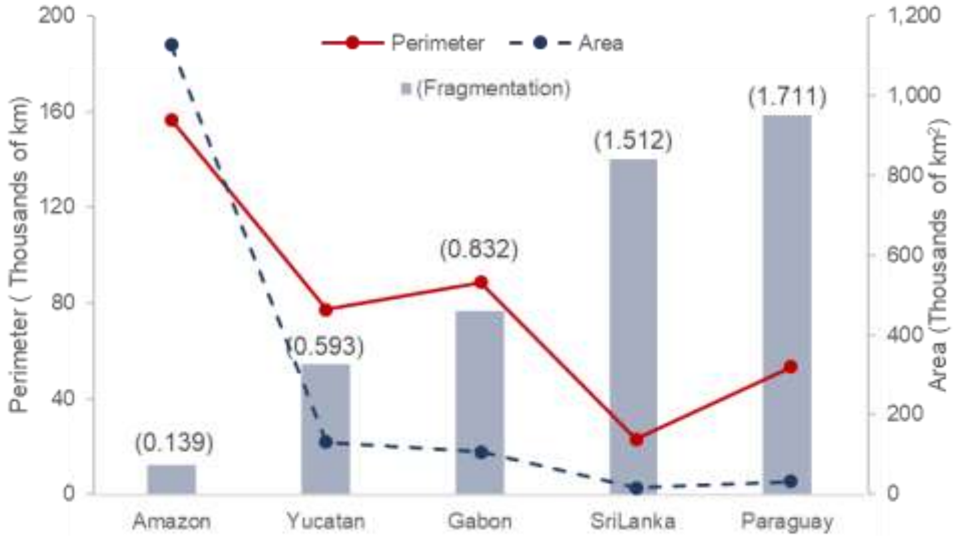


Figure 4.26. Regional fragmentation. A fragmentation index (1/km) was calculated as total perimeter (km) divided by total area (km^2) of forests patches (forest cover ≥50%) per region.

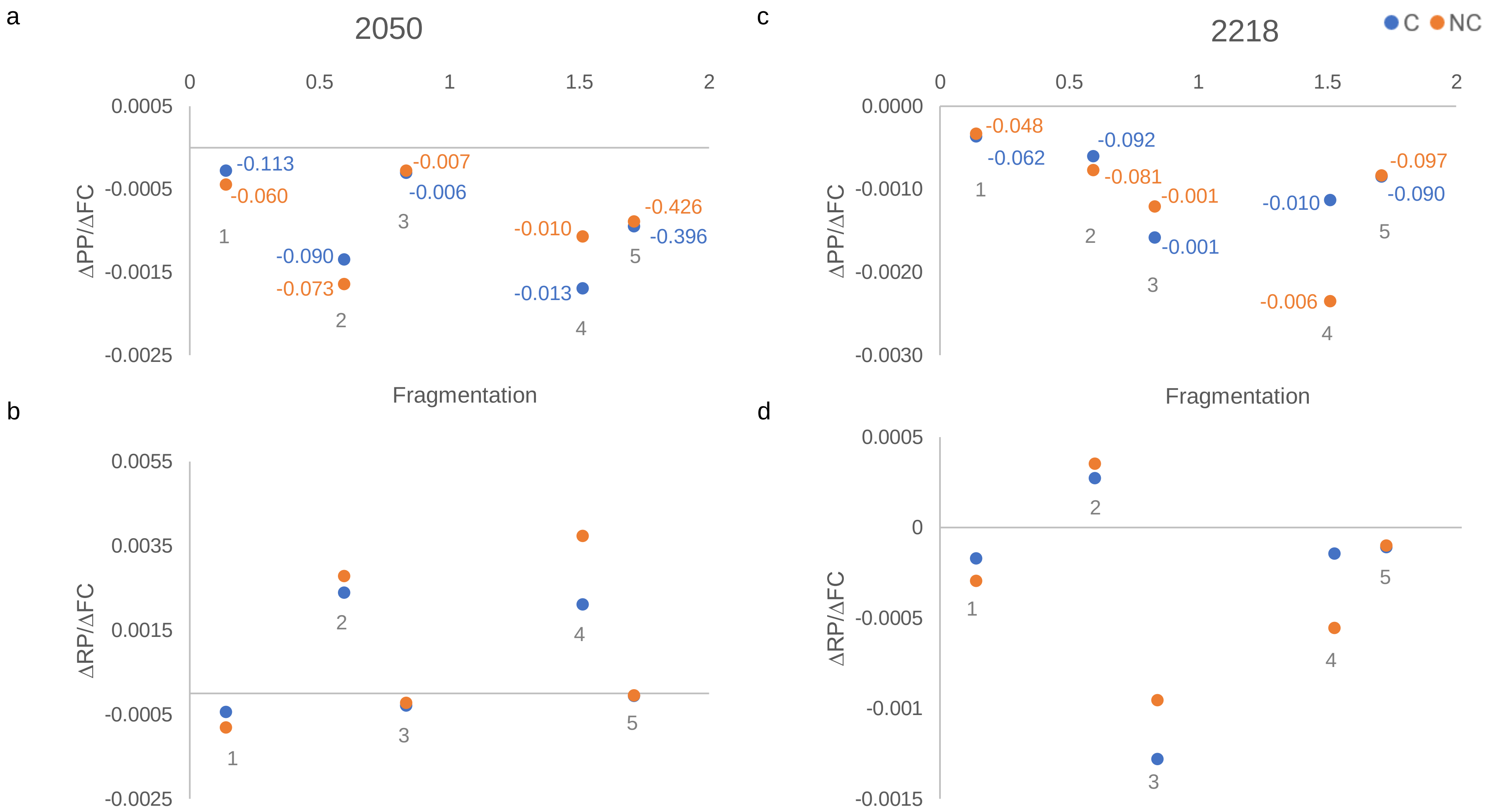


Figure 14.27. Relationship between fragmentation and change in service. a) Potential and b) realised pollination change per unit of forest lost in the short-term (2050) and c) potential and d) realised pollination change per unit of forest lost in the long term (2218) plotted against current fragmentation per region: 1. Amazon, 2. Yucatan, 3. Gabon, 4. Sri Lanka, 5. Paraguay. Numbers in colour are the estimated deforestation rates for conservation (C) and non-conservation (NC) scenarios.

4.3.3. Summary of regional results

Table 4.6. summarises results described in detail in section 4.3.2. for each of the regions where the effects of LUCC on potential and realised pollination service were assessed. This summary includes the mean values of potential pollination (PP), realised pollination (RP) and percentage of forest cover (FC) estimated at the present (baseline, BL), as well as the projected mean values for the year 2050 and 2218 under conservation (C) and non-conservation (NC) scenarios per region. The difference between the baseline (BL) and the scenarios mean values were calculated to identify a loss or gain of service in relationship with forest cover loss.

For all regions, a decrease in forest cover was projected, this varied in extent among regions and scenarios. In the case of the Amazon, the decrease in the percentage of forest cover was lower under the non-conservation scenario in both periods. In contrast, for Gabon and Paraguay, the decrease in the percentage of forest cover was lower under the conservation scenario. For Sri Lanka and Yucatan, a greater decrease was projected under the conservation scenario in the short-term but this changed in the long-term projection, where the higher decrement was projected under the non-conservation scenario.

A decrease in potential pollination is estimated for all regions in the short and long-term. In contrast, for realised pollination, Sri Lanka and Yucatan showed an increase in the short-term, and Yucatan showed it also in the long-term. Amazon, Gabon and Paraguay indicated a decrease of realised service from 2050 and Sri Lanka by 2218.

Regarding the relationship of change of potential pollination per each 1% of forest cover lost by 2050, under the conservation scenario, Sri Lanka presented the greatest loss followed by Paraguay, Yucatan, Gabon and Amazon. With no conservation conditions, Sri Lanka also had a greater loss, but Yucatan had a greater one over Paraguay and the Amazon over Gabon. In the long-term, in a conservation scenario, Gabon had the greatest loss, followed by Sri Lanka, Paraguay, Amazon and Yucatan the lowest. In a non-conservation scenario, Sri Lanka presented the greatest loss followed by Gabon, Paraguay, Yucatan and the Amazon.

In the case of realised pollination, the relationship of change of potential pollination per each 1% of forest cover lost by 2050, under conservation conditions, Amazon presented the highest reduction, followed by Gabon and Paraguay; whilst Sri Lanka showed an increase of service, followed by Yucatan. In a non-conservation scenario, the patterns of loss and gaining were the same as those of the conservation scenario. In the long-term, with conservation conditions, Gabon showed the greatest reduction followed by Amazon, Sri Lanka and Paraguay, only Yucatan showed an increase. Under non-conservation conditions, Gabon remained with the highest decrease, followed by Sri Lanka, Amazon and Paraguay, Yucatan, showed a higher increase under this scenario than under conservation conditions.

Table 4.6. Summary of results of regional analyses. Mean values of potential pollination (PP), realised pollination (RP) and percentage of forest cover (FC) in the present (baseline, BL), and projected in 2050 and 2218 under conservation (C) and non-conservation (NC) scenarios per region. Difference between the baseline values and scenarios values in 2050 and 2218, negative values represent a loss in service or forest cover (red) and positive values indicate a gaining (green). Value of pollination service difference (potential, ΔPP; realised, ΔRP) divided by the change in the percentage of forest cover loss (-ΔFC) indicates the amount of pollination service lost or gained due to the 1% loss of forest in the region.

		BL	**2050C**	**2050C-BL**	**2050NC**	**2050NC-BL**	**2218C**	**2218C-BL**	**2218NC**	**2218NC-BL**
Amazon	PP	0.02442	0.02342	-0.0010	0.02357	-0.00085	0.01994	-0.00448	0.02125	-0.00317
	RP	0.00656	0.00497	-0.0016	0.00501	-0.00155	0.00444	-0.00212	0.00372	-0.00284
	FC	72.38330	68.75320	-3.6301	70.45170	-1.93160	60.00500	-12.37830	62.76020	-9.62310
	ΔPP/-ΔFC			-0.00027		-0.00044		-0.00036		-0.00033
	ΔRP/-ΔFC			-0.00044		-0.00080		-0.00017		-0.00030
Gabon	PP	0.01079	0.01073	-0.0001	0.01073	-0.00006	0.01043	-0.00036	0.01049	-0.00030
	RP	0.00754	0.00749	-0.0001	0.00750	-0.00005	0.00725	-0.00029	0.00731	-0.00023
	FC	39.28070	39.09030	-0.1904	39.07250	-0.20820	39.05420	-0.22650	39.03510	-0.24560
	ΔPP/-ΔFC			-0.000332		-0.000274		-0.001581		-0.001208
	ΔRP/-ΔFC			-0.000290		-0.000221		-0.001281		-0.000954
Paraguay	PP	0.02028	0.00825	-0.0120	0.00819	-0.01209	0.00504	-0.01524	0.00407	-0.01621
	RP	0.00541	0.00457	-0.0008	0.00468	-0.00073	0.00346	-0.00195	0.00346	-0.00195
	FC	24.15820	11.48430	-12.6739	10.51040	-13.64780	6.12964	-18.02856	4.71786	-19.44034
	ΔPP/-ΔFC			-0.000949		-0.000886		-0.000845		-0.000834
	ΔRP/-ΔFC			-0.000066		-0.000108		-0.000053		-0.000100
Sri Lanka	PP	0.01883	0.01813	-0.0007	0.01849	-0.00034	0.01656	-0.00227	0.01591	-0.00292
	RP	0.01029	0.01115	0.0009	0.01147	0.00118	0.01000	-0.00029	0.00960	-0.00069
	FC	32.25940	31.85030	-0.4091	31.94360	-0.31580	30.25870	-2.00070	31.01850	-1.24090
	ΔPP/-ΔFC			-0.001693		-0.001070		-0.001132		-0.002350
	ΔRP/-ΔFC			0.002114		0.003734		-0.000146		-0.000555
Yucatán	PP	0.02011	0.01780	-0.0023	0.01784	-0.00227	0.01356	-0.00654	0.01274	-0.00736
	RP	0.00440	0.00849	0.0041	0.00823	0.00383	0.00736	0.00296	0.00777	0.00336
	FC	50.19420	47.30500	-2.8892	47.86910	-2.32510	31.88810	-18.30610	34.03990	-16.15430
	ΔPP/-ΔFC			-0.000798		-0.000975		-0.000357		-0.000456
	ΔRP/-ΔFC			0.001414		0.001648		0.000162		0.000208

4.3.4. Pantropical projected change of pollination service

A mean of 43.8% forest cover is currently estimated in the tropics. In the short term, greater forest loss is projected for a conservation scenario, 6.5% forest cover loss by 2050 compared to 5.9% forest cover loss in a non-conservation scenario. In the long-term projection, a lower forest cover loss is estimated for conservation compared to the non-conservation scenario, 14.4% loss by C2218 and 17.7% by NC2218 (Fig. 4.28a).

A decrease of potential pollination was projected for both scenarios compared to mean baseline pollination. Potential pollination was higher for the conservation scenario than for the non-conservation scenario (Fig. 4.28b).

An increase is projected for realised pollination under conservation conditions in the short term and a minor decrease in the long term compared to the baseline estimate. In contrast, a considerable decrease is estimated by 2050 under non-conservation conditions, by 2218 there is an increase compared to 2050, but is still lower than the baseline estimate (Fig. 4.28b).

Concerning the change of service per unit of forest loss (Fig. 4.28c), by 2050 the proportion of decrease of potential pollination is lower for conservation than for non-conservation scenario. In the long term, the difference between scenarios is reduced.

For realised pollination, there is a positive change in the short term under a conservation scenario and a considerable negative change under a non-conservation scenario. By 2218 the change is negative for both scenarios.

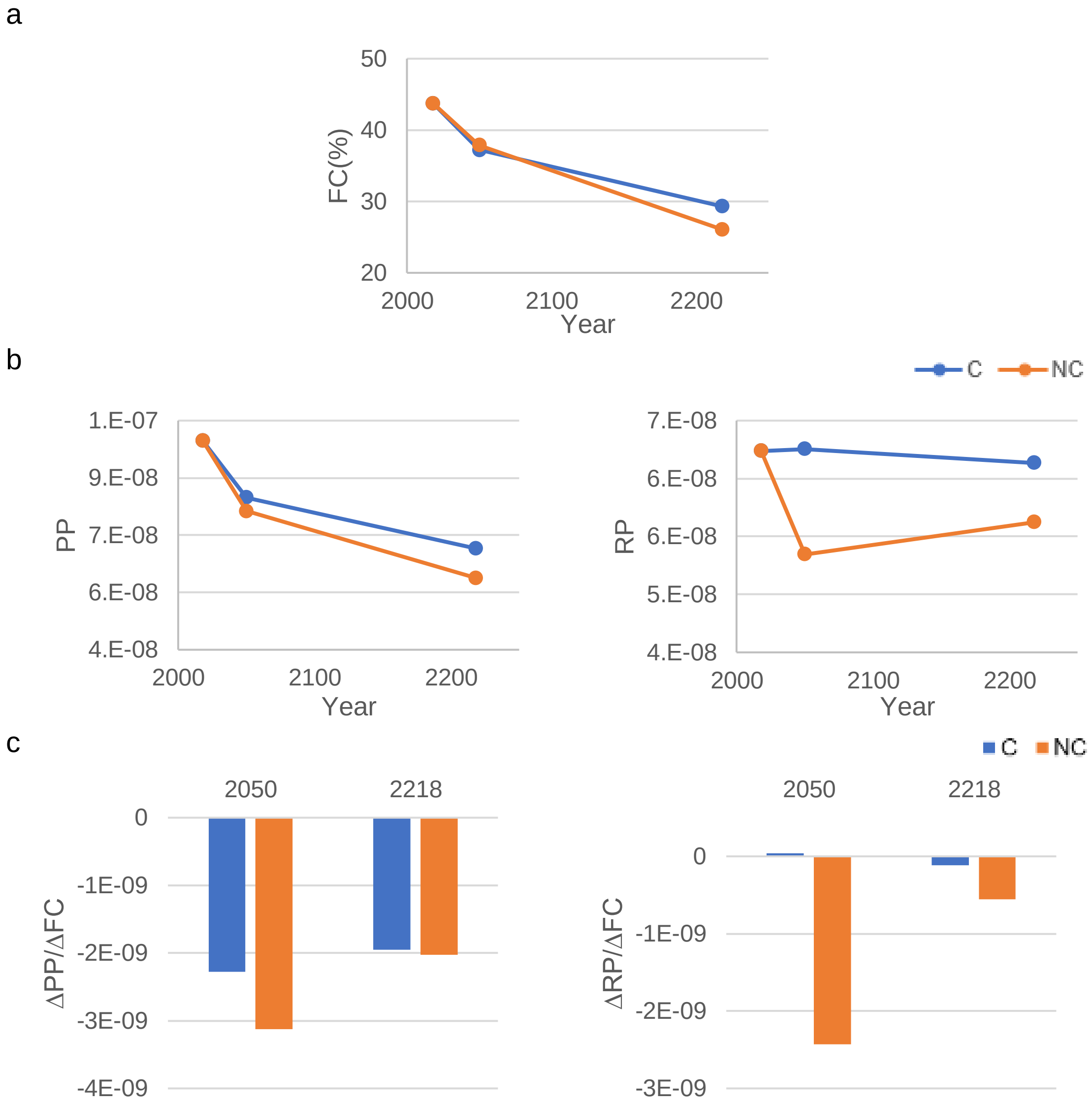


Figure 4.28. Pantropical change in pollination service. a) Forest cover, b) grand mean potential pollination (PP) and grand mean realised pollination (RP) and c) change in grand mean potential (ΔPP) and grand mean realised (ΔRP) pollination per unit of forest cover loss (ΔFC) for conservation (C) and non-conservation (NC) scenarios by 2050 and 2218.

In terms of the spatial distribution of change, a continuous loss of potential pollination was projected through time and practically all over the study area (Fig. 4.29). Some of the highest potential pollination values remained in the western Amazon Basin and central Africa forests, while the greatest losses were observed at the east of South America and South-East Asia.

Regarding realised pollination, the most notable change is the increase of the area of realised service, with projected service in Zambezian forest in Africa, Amazonian forest in America, and Polynesian forests in Asia from 2050. The conservation scenario showed higher realised pollination values than the non-conservation scenario (Fig. 4.30).

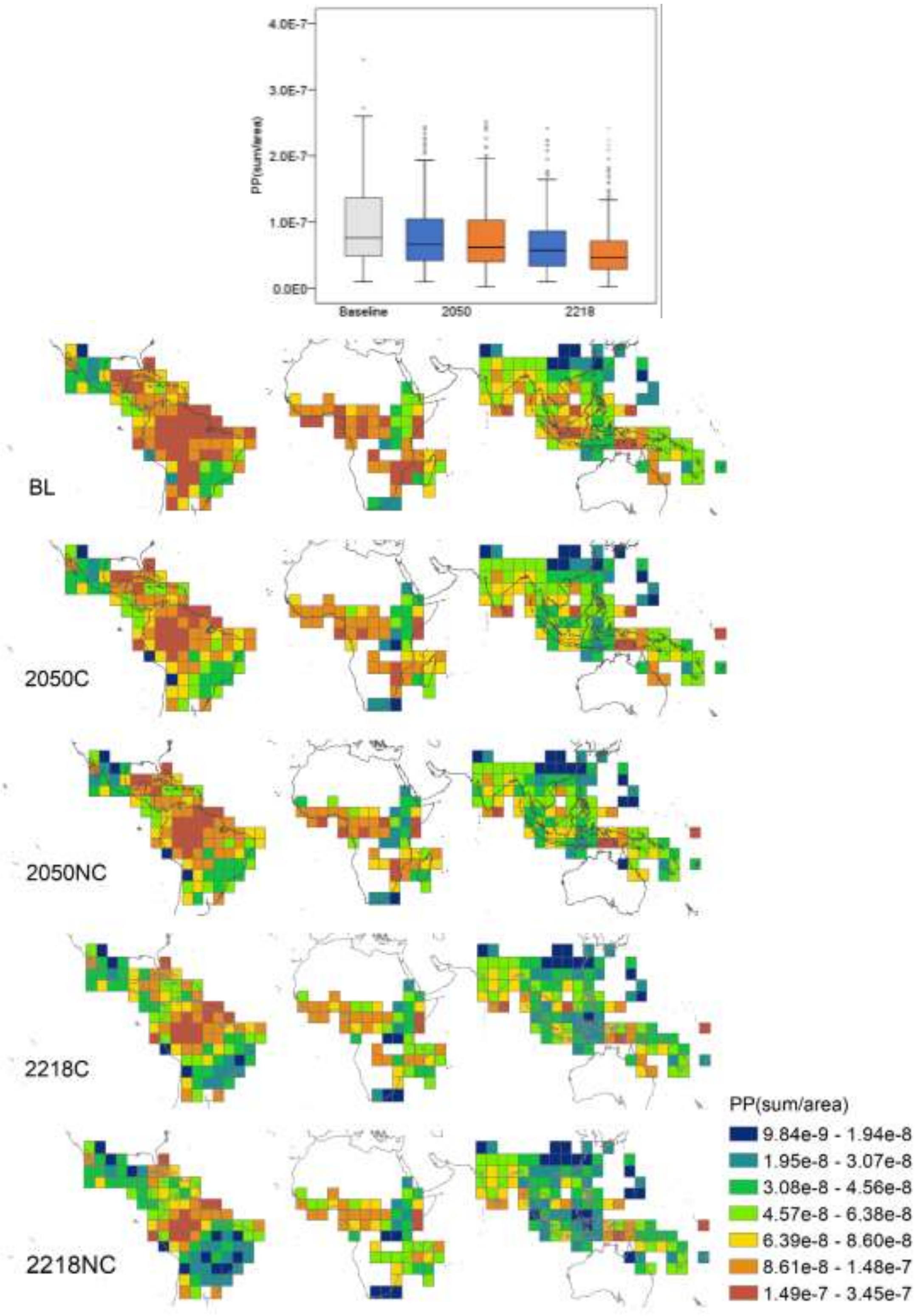


Figure 4.29. Pantropical projected potential pollination. Boxplot shows the distribution of mean potential pollination (PP) values per square corresponding to the baseline map (BL) and projected maps for conservation (2050C, 2218C) and non-conservation (2050NC, 2218NC) scenarios.

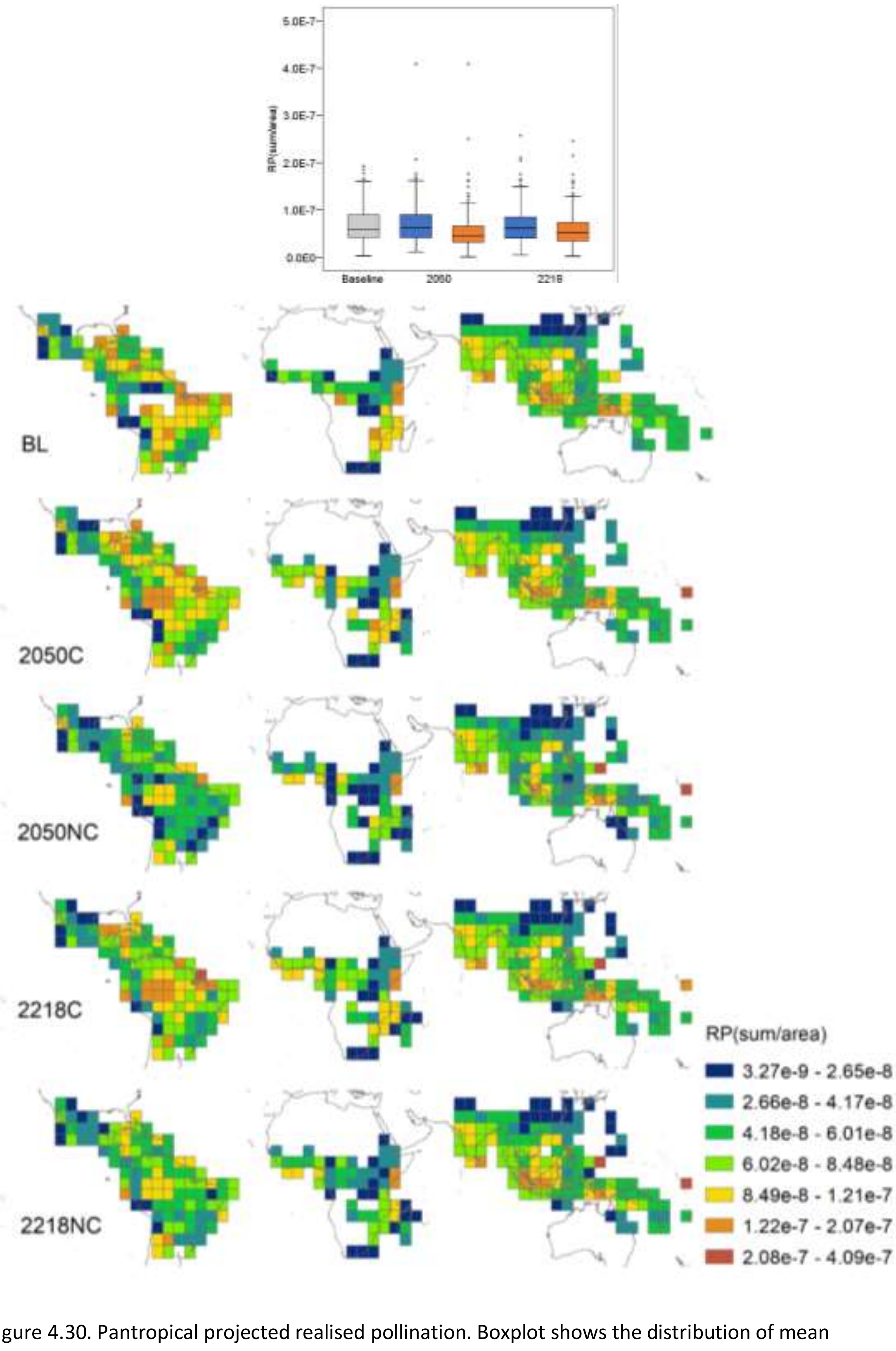


Figure 4.30. Pantropical projected realised pollination. Boxplot shows the distribution of mean realised pollination (RP) values per square corresponding to the baseline map (BL) and projected maps for conservation (2050C, 2218C) and non-conservation (2050NC, 2218NC) scenarios.

In terms of how the changes in service provision are distributed throughout the study area , for potential pollination (Fig. 4.31), the greater negative change occurred mostly in America and western Africa. In the short term, the Indochina region showed the lowest change in a conservation scenario, but a greater loss was projected for non-conservation conditions. In the long term, the change is similar for both scenarios.

Positive values resulted for some regions, for the equatorial African forest, this is explained by a negative change in potential pollination and a negative change in forest cover loss (i.e. forest cover gain, 0.07%) in the short term and in a non-conservation scenario in the long term. The rest of the positive values are explained by a positive change in potential pollination and projected forest cover loss for all scenarios.

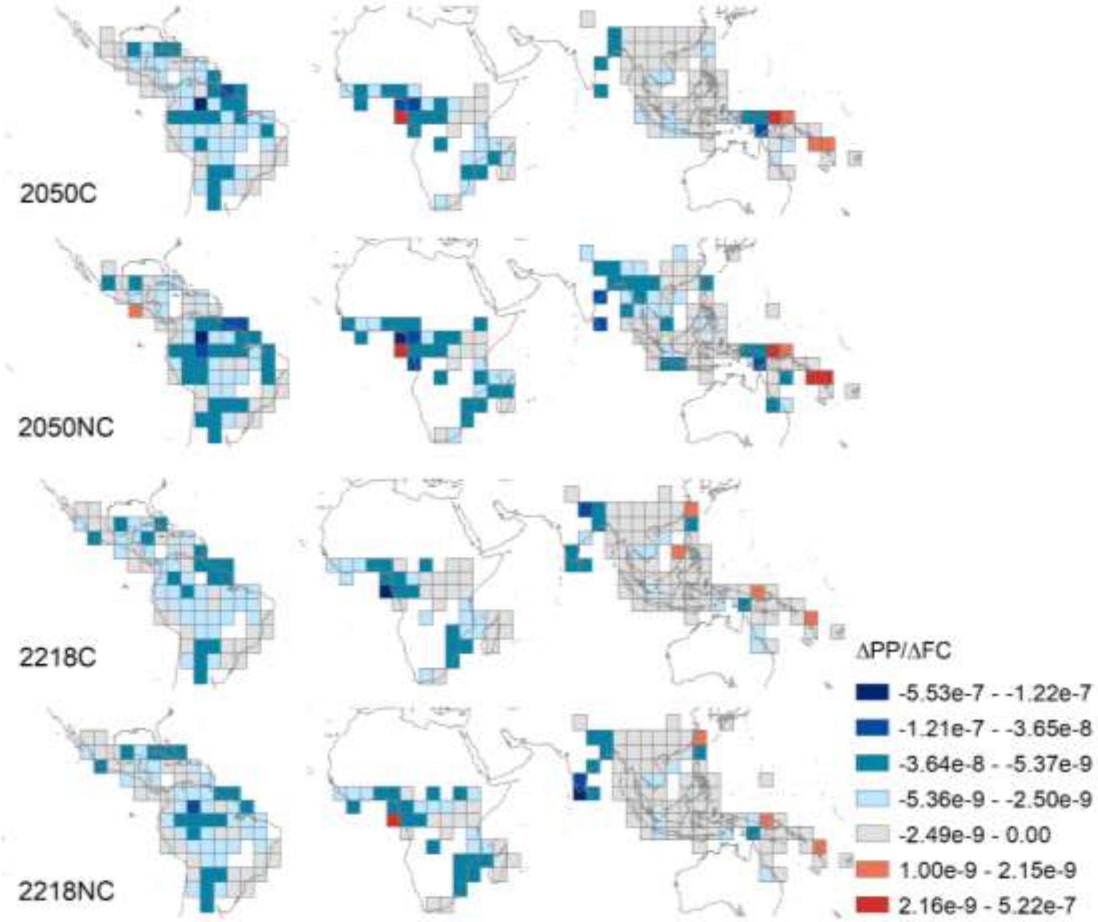


Figure 4.31. Projected change of potential pollination per unit of forest loss. Difference between the baseline and scenarios mean potential pollination (ΔPP) divided by the difference between baseline and scenarios mean forest cover (ΔFC).

Regarding realised pollination, positive and negative changes were projected throughout the tropics (Fig. 4.32). The greater negative change was projected under non-conservation conditions in the short term, while under a conservation scenario a maximum in realised service was projected. In the long term, the change in service is similarly distributed under both scenarios, although a negative change was projected in eastern China under a non-conservation scenario.

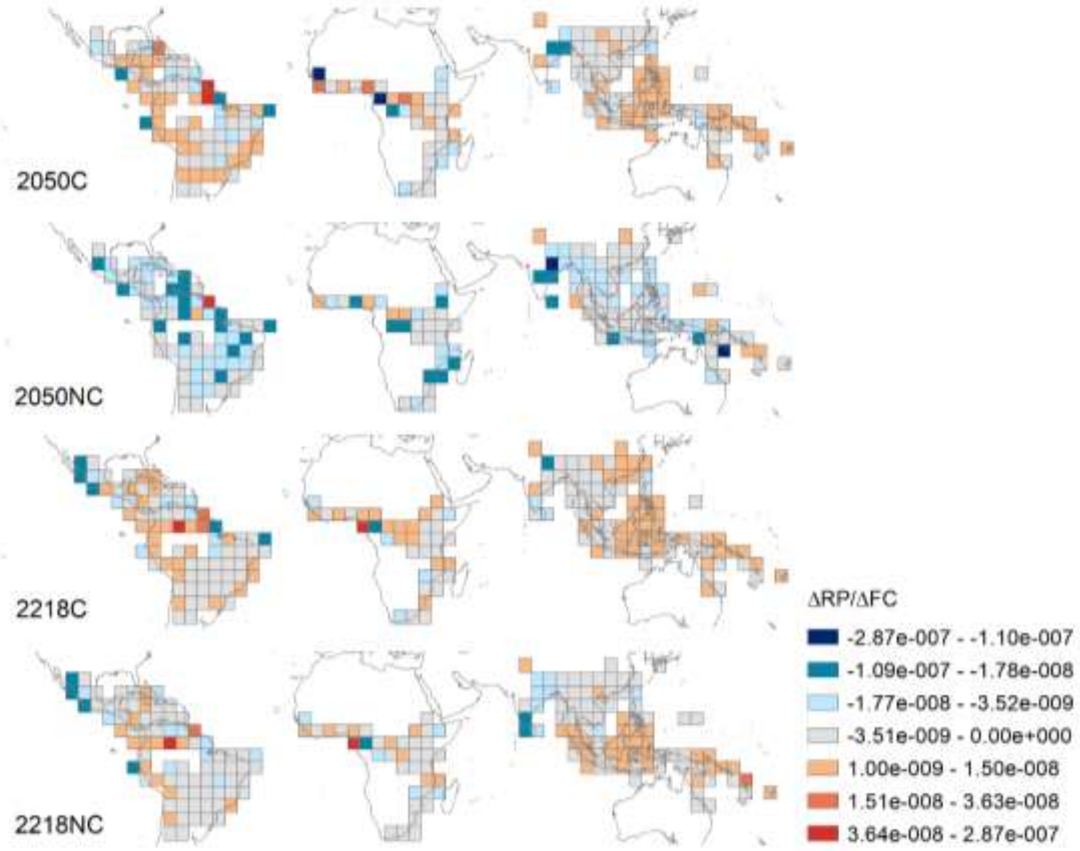


Figure 4.32. Projected change of realised pollination per unit of forest loss. Difference between the baseline and scenarios mean realised pollination (ΔRP) divided by the difference between baseline and scenarios mean forest cover (ΔFC).

The current mean pantropical fragmentation in areas with a ≥50% forest cover was 0.21 (Percentiles: 25%, 0.09; 50%,0.16; 75%, 0.25; Fig. 4.33a). The lowest fragmentation values occurred in the Amazonian forests (0.008-0.03) and central African forests (0.014-0.03), while the highest fragmentation values were in Mozambique coastal forests (0.903) and eastern China forests (1.065, Fig. 4.32b)

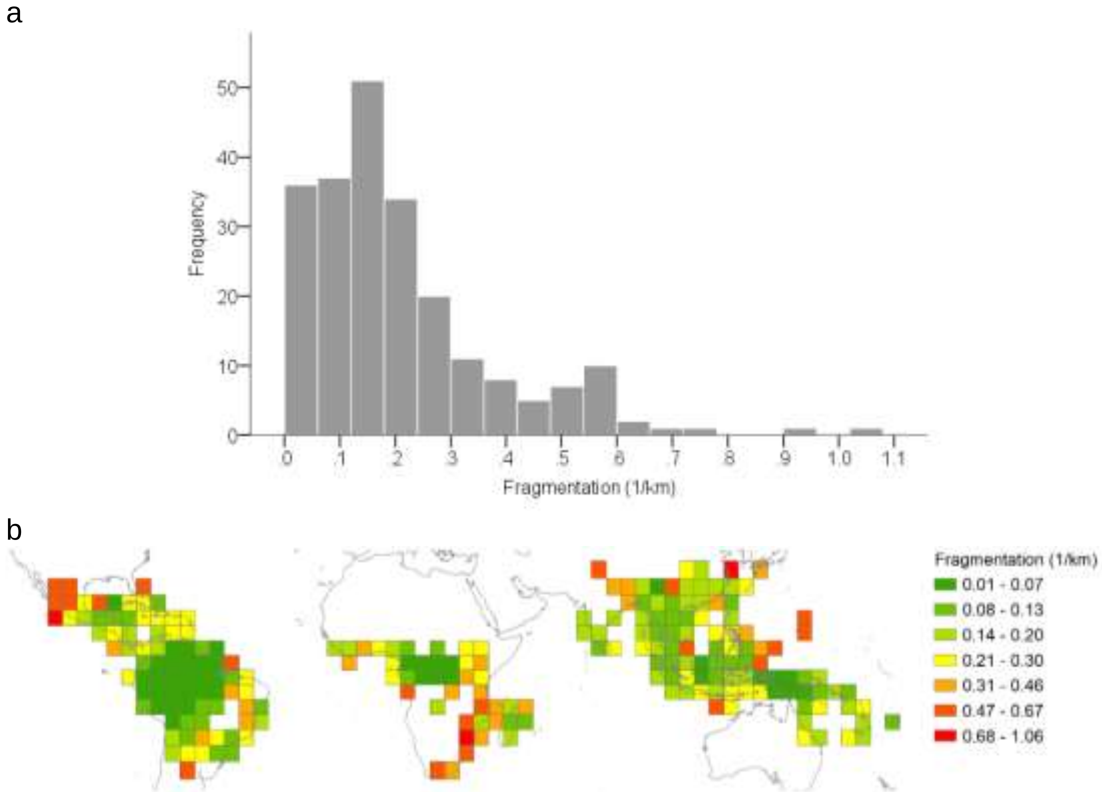


Figure 4.33. Pantropical fragmentation. a) Frequency and b) spatial distribution of fragmentation index (1/km) calculated as proportion of forest perimeter (km) per forest area (km^2) in regions with ≥50% forest cover.

When baseline mean change in service per unit of forest loss per square was plotted against their respective fragmentation index (Fig. 4.34), for 2050 projections, potential pollination results showed a positive trend for both scenarios (2050C, β=3.45e−8; 2050NC, β=3.02e−8). In the long term, a conservation scenario projection showed a negative relationship with fragmentation (β=−7.14e−9), while a non-conservation scenario presented a positive relationship (β=7.41e-9).

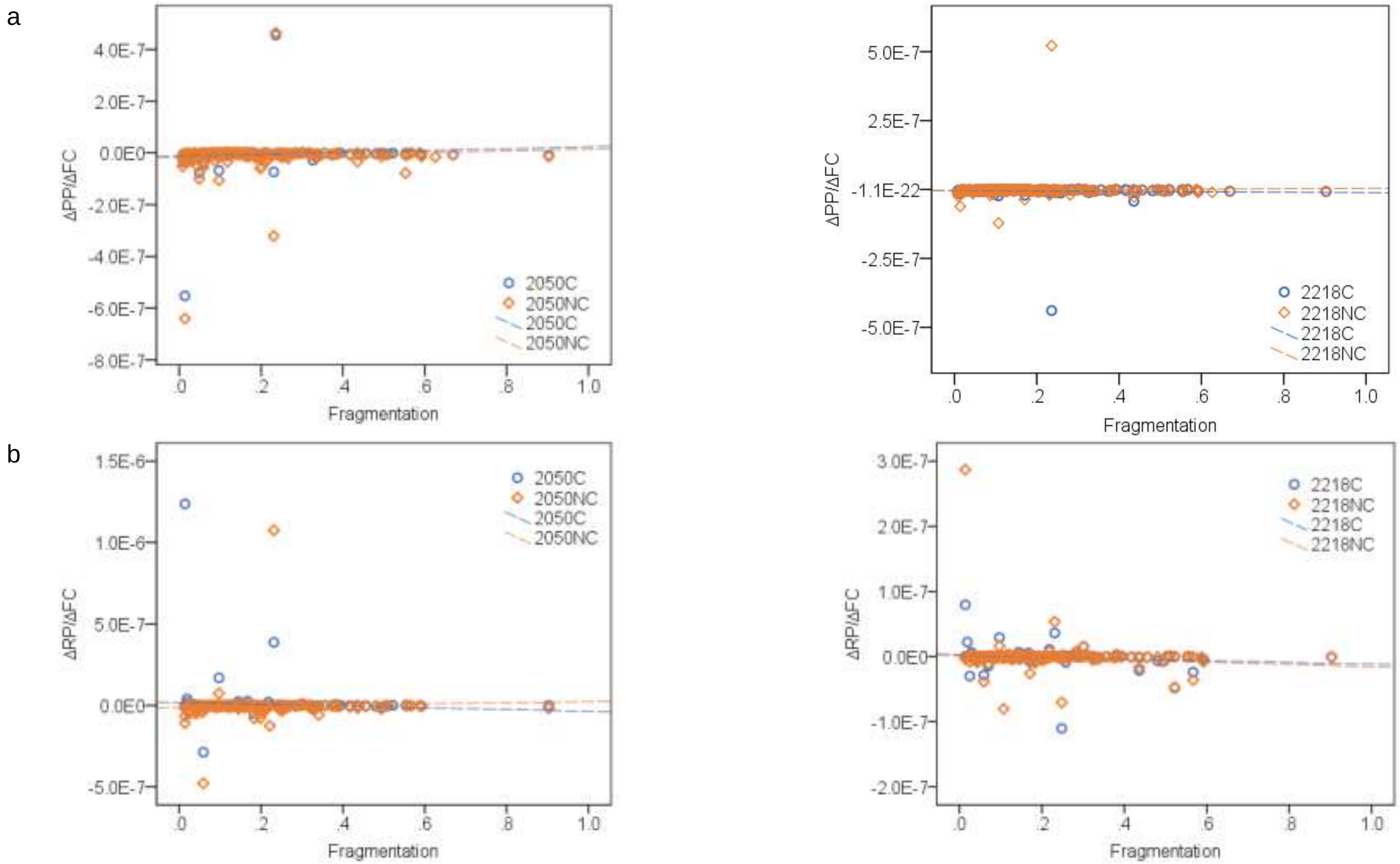


Figure 14.34. Relationship between fragmentation and change in service. a) Potential pollination change per unit of forest loss (ΔPP/ΔFC) estimated for 2050 and 2218 for conservation (C) and non-conservation (NC) scenarios plotted against current fragmentation index; R^2= 2050C, 0.01; 2050NC,0.005; 2218C,0.001; 2218NC, 0.0009. b) Realised pollination change per unit of forest loss (ΔRP/ΔFC); R^2= 2050C, 0.005; 2050NC,0.003; 2218C,0.024; 2218NC, 0.014.

Regarding realised pollination change, by 2050 a negative trend was suggested in a conservation scenario ($\beta=-5.37e-8$). In contrast, a positive trend is suggested for non-conservation conditions ($\beta=3.55e-8$). For both long term scenarios the relationship was negative (2218C, $\beta=-1.34e-8$; 2218NC ($\beta=-1.90e-8$). However, fragmentation showed a very weak non-significant linear relationship with change in services per unit of forest loss for all scenarios ($R^2<0.015$, $p>0.05$).

4.4. Discussion and conclusions

4.4.1. Effects of agriculturalisation on pollination services

In general, a decrease in potential pollination was suggested for all regions in the short term and continued in the long term, as result of the increase in the area of cropland, which is one of the least suitable land cover types for nesting and foraging (see Table 3.1). However, the response to the conservation and non-conservation scenarios varied among the regions as a result of the proportion of cropland vs mosaic vegetation area (Fig. 4.10). While the loss of service was lessened under a conservation scenario in the Amazon and Yucatan, it was greater for Gabon, Paraguay and Sri Lanka. These last three sites have a lower forest cover, mostly restricted to protected areas, than the Amazon and Yucatan. Under a non-conservation scenario, in Gabon, Paraguay and Sri Lanka, deforestation was allocated to pixels within protected areas with a higher forest cover. Therefore, the proportion of pixels converted to mosaic vegetation (a more suitable land cover type for nesting and foraging) was greater than area converted to cropland (the least suitable land cover type, Fig. 4.10).

In contrast, a conservation scenario increased the area of cropland-only cover type, given the relatively low percentage of forest cover outside protected areas of these three regions. This is not the case for the Amazon and Yucatan, where a conservation scenario maintained the service within protected forests and still presented a mosaic vegetation cover type outside them, given the higher forest cover present in these two sites.

In the long term, the projected forest loss in Gabon and Paraguay is not considerably greater than the projected in the short term and was similar between scenarios, therefore a lower change in service continued under a non-conservation scenario. In the case of Paraguay, the highest deforestation period was estimated from 2001 to 2012 (Baumann et al. 2017), assuming BAU, the greatest forest cover loss could occur by 2050, meaning that conditions by 2218 would be similar to the suggested in the short term. In contrast, in Sri Lanka areas that once benefited from a mosaic vegetation cover turned into less suitable landcover type in the long term under the non-conservation scenario.

The theoretical negative relationship between the provision of regulation services and level of anthropogenic disturbance (de Groot et al. 2010, Cimon-Morin et al. 2013) was observed for potential pollination service for all regions (see Table 4.6). However, this is not the case of realised service, where projections suggested a gaining in service for Sri Lanka and Yucatan in the short term compared to baseline estimation, and for Yucatan in the long term as well. Instead of a linear negative relationship, these regions showed a curvilinear relationship, indicating that they have not reached a maximum in realised service. These projections can help to identify where and when an inflexion point could be reached and turn into a loss of service. Also, they are useful to understand at what extent the protection of forests would prevent or slow down this loss, as suggested by the Sri Lanka conservation scenario.

Similar to regional trends of change, potential pollination showed a general decrease in service at pantropical scale, especially in a non-conservation scenario, and changed rapidly in the short term. Potential pollination loss could have major negative consequences for wild plant communities all over the tropics. Given the high reproductive diversity of flowering plants on animal pollination, a decline in pollination would imply disruption in ecosystems functioning due to the loss of habitat and food resources for a wide range of species (Potts et al. 2016), including biodiversity hotspot areas. Although a conservation scenario could considerably reduce the loss in the short and long terms, a decrease in deforestation rates and an increase in forest protection are necessary to maintain current potential pollination through time.

Regarding realised pollination, the exclusion of deforestation in protected areas is suggested as the way to maintain pollination to tropical crops in the long term. Although some regions could benefit in the short term from wild insect pollination, this could lead to a decrease in service at pantropical scale in the long term. Therefore, a conservation scenario is suggested as the less detrimental for natural and agroecosystems regarding pollination service. As for potential pollination, restraint of deforestation outside protected areas would not prevent the loss.

While protected forest showed to have a relevant role in reducing the loss of pollination service, avoidance of deforestation within protected areas is not enough to stop service reduction. Furthermore, evidence suggests that environmental changes within tropical protected areas are strongly linked to their surrounding habitats, and broad-scale loss and degradation of such habitats could increase the likelihood of biodiversity decline (Laurance et al. 2012) and ecosystem services loss. Sustainable agricultural practices, such as sustainable intensification, conservation agriculture, and agroforestry, along with avoidance of agricultural expansion into native habitats are essential to avoid further degradation of natural ecosystems (IPBES 2018).

Proximity to forests increased the probability of realised service occurrence. Therefore, pixels adjacent to protected areas or with a projected mosaic cover type presented higher values than extensive areas of cropland, such as the projected for Paraguay. Based on the idea that an increase in edge length of forest patches would increase the probability of service and that future deforestation patterns were defined by current deforestation fronts, a positive relationship between fragmentation and a service gain was expected, particularly for a non-conservation scenario, where deforestation in highly forested areas was allowed. However, no strong relationship was identified.

This was a simple approach to assess the relationship between baseline fragmentation with service change, the inclusion variables other than total forest patch perimeter could improve the understanding of the difference in realised service change among regions, such as proximity among patches and forest type. Also, further assessment of the difference in future fragmentation patterns derived from alternative scenarios is required.

Along with LUCC, climate change has a significant impact on ecosystem services and it will be exacerbated in the future (Mooney et al. 2009). A systematic review carried out by Runting et al. (2017) on the impacts of climate change on ecosystem services (117) showed that 59% of the analyses were negative, 24% mixed, 13% positive and 4% neutral. Regulating services (e.g. pollination, biological control) and cultural services (e.g. tourism, aesthetic appreciation) are more negatively impacted by climate change than provisioning services (e.g. food, raw materials).

Regarding pollination service, climate change has been identified, along with LUCC, as a major threat to wild pollinator populations (Schweiger et al. 2010). Some of the effects identified due to a gradual climate change are phenological decoupling of plant-pollinator mutualism, landscape alteration, climate-driven shifts in ranges and competition with non-native species (Chen et al. 2011, Kerr et al. 2015, Settele et al. 2016). Meanwhile, the effects identified due to extreme wheater events caused by climate change are the decline of populations, the decrease in breeding success and floral resources, alteration of foraging patterns and spreading of pathogens (Giannini et al. 2012, Settele et al. 2016, Erenler et al. 2020). Therefore, to assess the future condition of pollination service (or any other ecosystem service) is necessary to consider the effects of both LUCC and climate change.

The effects of climate change could be incorporated in the pollination model using alternative climatic data and scenarios (e.g. Nakicenovic et al. 2000, van Vuuren et al. 2011). Modification of climatic data would have a direct influence on the foraging activity variable, given its relationship with temperature and solar radiation. Equally, climate change may alter significantly distribution plant taxa (Shafer et al. 2015) and thereby major vegetation cover types (i.e. tree, herb, bare; Notaro et al. 2007). Data related to the percentage of change in vegetation cover type as a result of climate change could be incorporated in the QUICKLUC model settings.

To understand the future condition of ecosystem services is imperative to understand the impacts of both LUCC and climate change. To predict the effects of LUCC and climate change it is important to consider not only the biophysical aspects (e.g. temperature and precipitation), but also the socioeconomic changes (e.g. increase in population, food demand, and technology) as well as changes in policy and institutions (MA 2005). However, the impacts of future LUCC and climate change can be difficult to assess as these often change over long timescales with high uncertainties (IPCC 2014). This must be considered in the interpretation of results provided by LUCC and climate change models.

4.4.2. Assumptions and limitations of the model

The data and settings used to model LUCC carry several assumptions that must be considered when concluding the effects of LUCC on pollination services. First, the Global Forest Cover dataset considers forests as any vegetation higher than 5m and covers above 10% of a pixel (Hansen et al. 2013), it includes both natural forest and tree plantations. Evidence suggests that foraging activity of wild bees and other wild insect pollinators is lower in tree plantations than in natural habitats (e.g. Lander et al. 2009, Freitas et al. 2014, Kaluza et al. 2016). Therefore, an overestimation of pollination service is possible when assigning equal suitability for nesting and foraging in undifferentiated tree cover of natural habitats and forest plantations.

Second, it is important to consider that this analysis was limited to assess the effect of agriculturalisation on service provision and no other LUCC processes were included in the model. The LUCC model was set to project deforestation (tree cover loss) only, and to be allocated based on agricultural suitability to cropland only. Afforestation (tree cover gain), change in herb and bare cover percentages, allocation of grazing or protected land instead of cropland, were not included in the assessment. For regions such as central Africa forest, where afforestation has been observed (Aleman et al. 2018), or regions where new protected areas could be declared (Bacon et al. 2019), these results might vary. Therefore, further assessment of other LUCC processes is required.

Third, the main difference between scenarios was the absolute exclusion of deforestation in protected areas in the conservation scenario defined by 100% management effectiveness. Thus, it is assumed that no further deforestation will occur within protected areas. However, agriculturalisation within protected areas is recognised (see section 3.2.2, IUCN categories of protected areas), and the expansion of agricultural is possible. Although this could be accounted for in the model by changing the management effectiveness index, it was preferred to consider a scenario where conservation was privileged over other processes and be able to generalise for all protected areas. Management decisions and effectiveness are highly variable in space and time (Danielsen et al. 2005, Dudley 2008) and it could be considered when analysing a particular area at a given time.

Equally, deforestation rates were assumed to remain constant in the future, i.e. assuming the current socioeconomic conditions will not change in the future. Although new transport routes were included in the scenarios settings, other factors that could affect the occurrence of deforestation fronts, such as population growth, an increase in food demand or implementation of new technology were not considered in the model settings. While assuming constant conditions in the short-term projections is plausible, it is not possible to extend this assumption to the long term (IPCC 2014). The long-term scenarios allowed to identify the different inflexion points of provision and demand of pollination service among regions and throughout the tropics, showing that different baseline conditions influence the model outcomes, and do not necessarily involve service loss. However, it should be noted that current conditions are unlikely to remain for the next 200 years.

A limitation of the analysis was the lack of the future distribution of pollinator-dependent cropland to accurately project realised pollination service. Some studies have assessed the future distribution of major crops (e.g. maize, wheat, Bradley et al. 2012, Estes et al. 2013). However, this information was not available to carry out the analyses using a specific distribution of pollinator-dependent crops and a general cropland distribution was used instead. This was considered a fair approximation because the ‘Geographic distribution of major crops across the World’ map (Leff et al. 2004), shows a mixed distribution of major crops with pollinator-dependent crops, but this certainly can be improved if the required data becomes available.

Equally, to obtain a pantropical-scale estimation of change it was a required upscaling the resolution of the pantropical scale analyses, due to the computing time and data storage limitation. This implied the homogenisation of the effects of LUCC on pollinations service over a much wider area (10 km^2) compared to the regional analyses (1 km^2). This still allowed to fulfil the aim of the analyses, a lower resolution allowed to identify general patterns of distribution of change at a wider scale, while a higher resolution allowed the comparison among regions. A wide-scale high-resolution analysis can be achieved if the computing infrastructure is available.

4.4.3. Conclusion

In conclusion, the exclusion of deforestation in tropical protected areas had differential outcomes of realised pollination services among the regions and between time scales. In contrast, a decrease in potential service was observed for all areas and pantropically in both scenarios in the short-term. Assuming unchanged future conditions, a conservation scenario would not maintain current provision and distribution of pollination service but would result in a minor loss compared to a non-conservation scenario. Further assessment is required to analyse the relationship between fragmentation and change in pollination services.

This chapter showed how LUCC models can be used to analyse the effects of LUCC on an ecosystem service at different spatial and temporal scales. However, it is important to consider the assumptions made and recognize the limitations of the models when interpreting the results. These kinds of analyses can be used to estimate the change in ecosystem service provision and to assess the change in its spatial distribution. This information can be useful to inform conservation and management decisions.

5 A blueprint for modelling pest control and seed dispersal at pan-tropical scale

5.1. Introduction

A wide range of ES are required to secure human well-being and dependency on them will continue to increase in time (Lin et al. 2018). Although this has been widely recognised (Costanza et al. 2017), the spatial synergies and trade-offs among ES are still scarcely understood (Mouchet et al. 2014). Spatial ES models are useful tools to assess this relationship and to prioritize areas that will allow multiple management and conservation goals (Martínez-Harms and Balvanera 2012).

As discussed above (section 3.2.3), focusing on a single ES spatial models can provide detailed insight into the process and improve the understanding of service distribution and effects of environmental changes. However, focusing on a single ES can minimize the benefits obtained through a range of ES and potentially lead to the creation of dysfunctional incentives (Costanza et al. 2017) that work against improving the benefits that we receive from nature. Most ES are produced as joint products (or bundles) from intact ecosystems, these vary among systems, sites and times. It is necessary to consider the full range of services and the characteristics of their bundling to maximize the net benefits to society (Costanza et al. 2017). For example, focusing only on the carbon sequestration service of a forest may in some instances reduce the overall value of the full range of ES, such as the provision of raw materials or tourism. Therefore, as emphasised before, faunal ecosystem services (FES) should be considered as part of the bundle of services in management and conservation strategies.

While assessing multiple ES can maximize the benefits, it is also a challenging task, particularly in the spatial dimension. Currently, the understanding of the spatial interactions among ES is relatively limited (Lin et al. 2018). Particularly for FES, although the benefits are tangible (Gutierrez-Arellano and Mulligan 2018), the processes by which these benefits are produced spatially are complex and scarcely understood (Harrison 2017, Rega et al. 2018).

Along with pollination distribution models, a few spatially explicit models have been developed to map natural pest control and seed dispersal. These are taken as a reference to assess the possibility of developing a natural pest control and seed dispersal models at the pantropical scale. Taking a similar approach to the one used to model pantropical pollination, the creation of pantropical pest control and seed dispersal model is proposed here. This chapter describes tentative modelling approaches for these FES based on the ecological theory that explains the processes that underpin them, current data availability, and the challenges involved in this task. To conclude, the aim to integrate them to produce a pantropical model of some FES is discussed.

5.2. Natural pest control

Natural pest control service—also known as biological control or biocontrol— results from the interaction between populations of natural enemies. Among the best-known interactions from the ecological theory perspective are predation and parasitoidism (e.g. Mills and Getz 1996, Briggs and Hoopes 2004). Unlike other antagonistic interactions, such as parasitism or competition, the definitive outcome of predation and parasitoidism is the mortality of some individuals of one well-identified population.

In the case of predation, the prey is killed and eaten by the predator. In the case of parasitoidism, the parasitoid lays eggs on or in the body of the host killing it eventually. As summarised in Chapter 2, the identified providers of natural pest control to crops are insectivorous insects, birds and bats, performing as predators, and some wasps and flies, performing as parasitoids.

The outcome of these interactions has allowed the development of ecological models using differential equations. The Lotka-Volterra models (Lotka 1925, Volterra 1926) and Nicholson-Bailey Model (Nicholson and Bailey 1935) —and subsequent development and modifications of models— offer a fair understanding of the mechanisms determining the populations' sizes of the actor populations. Out of these two interactions, parasitoidism is probably the one that allows more simplifying assumptions, as this is provided only by sexually mature female individuals.

These models consider a two-species relationship occurring in isolation, without considering the complex links of both actors with their surroundings (Gutierrez et al. 1994), which most probably explains the difference between the outcomes predicted by the models from those observed in the field (Mills and Getz 1996). The extensive ecological knowledge on this process offers a good baseline to explore its relationship with land use and landscape complexity (Jonsson et al. 2014).

Compared with managed pollination, managed natural pest control has had a relatively lower success rate. According to the review provided by Greathead and Greathead (1992) on the introduction of natural enemies to eliminate crop pests around the world (196 countries) since mid-nineteenth century to the late twentieth century, only 30% of the introductions have resulted in the establishment of the natural enemy in the target region and only 12% have resulted in substantial or complete control of the target pest. Also, some introductions have produced negative consequences for non-target native species (Simberloff and Stiling 1996). Since the understanding of successful managed natural pest control is still limited, wild predator/parasitoid populations play a fundamental role as service providers to reduce production costs and use of chemical pest control —and the negative impacts this causes (Gutierrez-Arellano and Mulligan 2018).

Like pollination, species richness is an important attribute in specialist relationships (Letourneau et al. 2015), but abundance is the determinant factor for natural pest control to cropland (Maas et al. 2013, Winfree et al. 2015). A recent global study by Dainese et al. (2019) suggests that richness and abundance of natural enemies have a positive effect on natural pest control delivery. Equally, the distance from natural habitat, land cover type and spatial configuration have been identified as the most explanatory variables of providers abundance (Railsback and Johnson 2014, Letourneau et al. 2015). Based on this, some natural pest control spatial models have been suggested.

5.2.1. Available spatial models

Some advances in modelling natural pest control distribution have been carried out in the last decade, the methodological approaches include participatory mapping, biophysical indicators and spatial simulation. The geographical scales represented range from local to continental and are mostly located within Europe (Table 5.1).

First approaches to analyse pest control services to cropland spatially were done by Raymond et al. (2009) in the Murray–Darling Basin in South Australia using a participatory GIS approach, where community members of the study area were asked to spatially locate and assign a value to a range of ecosystem services, including natural pest control. This was used later to compare ecological and social values for natural areas in the same site (Bryan et al. 2011). These studies identified natural pest control as highly valuable and threatened in the area. Although these studies show the utility of participatory mapping as a first approach to understand the value and distribution of regulating services, these outcomes require further assessment to identify the patterns of spatial distribution.

Landscape scale

A spatial quantitative assessment was carried out by Petz and van Oudenhoven (2012) in the Groene Woud area, in the Netherlands. Natural pest control is one of eight services assessed. Based on the available evidence suggesting a positive relationship between insect pests predation rate and area (in hectares) of forest edges, i.e. area of forest in 25 x 25 m grids that contained both forest and non-forest habitat types. (Levie et al. 2005, Bianchi et al. 2006, Bianchi et al. 2008), they mapped the density of forest and hedgerows within a 1000 m distance from cropland as an indicator of service provision.

Also at a landscape scale, Jonsson et al. (2014) developed a mechanistic model based on a conceptual framework which incorporates plant, herbivore (pest) and natural enemy (service providers) communities with land use and landscape structure in a geographical context. They apply the model to aphid pests in cereal crops, parameterised for Uppland, Southern Sweden. They also consider predation as a pest control mechanism, provided mainly by spiders and beetles. Based on evidence suggesting a high correlation between different land cover types and abundance of pest control providers (Bianchi et al. 2006, Chaplin-Kramer et al. 2011), Jonsson et al. (2014) used the CORINE land cover dataset to generate two variables, proportion of land not covered by annual crops and the proportion of grassland within 135, 500 and 1500 m from cropland. The study included sensitivity and validation analyses. Their results suggest higher service provision in landscapes with a higher proportion of non-cropland cover for all radii (Fig. 5.1a).

Table 5.1. Natural pest control spatial models. Recent spatially explicit models of natural pest control services, scale, resolution and study area where the models were applied, if these model were part of a single-service (S) or a multiple-service (M) assessments, the variables used and the potential proxy data to model natural pest control at pantropical scale.

Model	Scale	Resolution	Study area	S/M	Variables	Pantropical proxy
Raymond et al. (2009) Bryan et al. (2011)	Regional	100m	Murray–Darling Basin, Australia	M	Occurrence/absence of pest	Literature review
Petz and van Oudenhoven (2012)	Landscape	25 m	Groene Woud, the Netherlands	M	Forested area	Forest cover
Jonsson et al. (2014)	Landscape	25m	Uppland, Sweden	S	Mean annual temperature Proportion of non-cropland Proportion of grassland	Global climate data Non-cropland land cover
Collard et al. (2018)	Plot	0.4m	Simulated plots	S	Crop edge length Aggregation of non-crop habitat Percentage of non-crop habitat Proximity to non-crop habitat	Cropland land cover Non-cropland land cover
Rega et al. (2018)	Continental	100m	Europe	S	Seminatural habitat cover types Spatial configuration of non-crop habitats Vegetation structure	Global land cover types

Plot scale

Collard et al. (2018) provide a theoretical contribution on the effect of spatial configuration of non-crop habitats to enhance natural pest control services. They used landscape ecology metrics to generate over 1700 simulated agricultural plots varying in percentage, aggregation, proximity and edge length of favourable (non-crop) habitat for predators. Then, they developed an individual-based model to simulate foraging activity based on literature and personal observations of the banana weevil (pest)- earwig (predator) interactions, which they suggest can be extended to many species of ground-dwelling generalist predators, such as ants, ground beetles and spiders. They found that an increase in the percentage of non-crop habitat and aggregation resulted in the spatial dilution of predators, and this is effectively counteracted by the increase of edge length. Thus, they identified non-crop habitat strips among banana plant rows as the best spatial configuration for service provision (Fig. 5.1b).

Pan-European scale

In the opposite side of the spatial scale spectrum, Rega et al. (2018) modelled the pan-European distribution of natural pest control combining geospatial layers and information derived from field surveys. This model quantifies the potential service provision for a given landscape rather than the final service delivery (reduction in pest density, higher crop yield), which is highly context-dependent. The model depicts provision from flying predators and parasitoids, adopting a 500 m maximum flight distance and a normal distribution as a distance weighted function for service provision. Based on a scoring system derived from an extensive field survey (Moonen et al. 2016), they classified European seminatural habitats into five classes considering vegetation structure and spatial configuration —lower to higher scores: herbaceous area, herbaceous linear, woody areal-edge, woody areal-interior and woody linear (Fig. 5.1c). The output map shows that a large proportion of highly productive agricultural areas has a low potential for natural pest control.

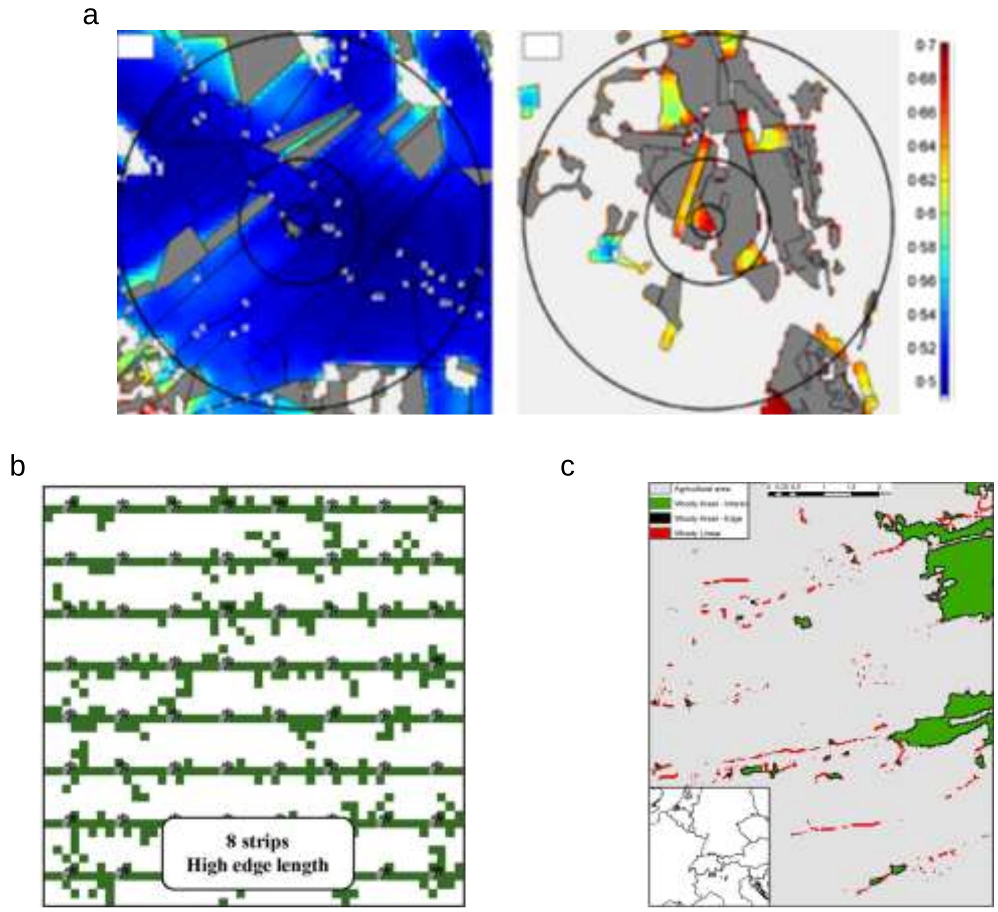


Figure 5.1. Land cover and spatial configuration in natural pest control models. a) Predicted service in Uppland, Sweden by Jonsson et al. (2014), cropland is marked with a colour gradient, depending on the service predicted (low, dark blue to high, dark red). A landscape (left) dominated by annual crops shows less predicted service than a landscape (right) dominated by grassland (dark grey) and forest (light grey). b) Example of a simulated plot by Collard et al. (2018) with the best spatial configuration for service provision, with natural habitats in green, unfavourable habitat in white and crop (banana plant) in grey. c) Classification of seminatural habitats in Europe by Rega et al. (2018) according to their potential to provide service, in lower to higher-order: agricultural land (grey), woody areal-interior (green), woody areal-edge(black) and woody linear (red).

5.2.2. Modelling pantropical natural pest control

Table 5.1 summarizes the main characteristics of the available models and allows a better understanding of the opportunities to generate a pantropical pest control model. First, regarding the spatial scale, there is a representation from local (plot) to the continental scale. This shows the feasibility to assess the distribution of this FES at pantropical scale bearing in mind the limitations of the outcome. While a plot scale model can provide detailed information on the reduction of pest density or target crop viability (Collard et al. 2018), a regional or continental scale model can provide an estimate of providers abundance (Rega et al. 2018), as is the case with the pantropical pollination model.

Concerning resolution, coverage vs. fine-grained resolution is a common trade-off in spatial models, a high spatial resolution often means lower spatial coverage and vice versa. At broad scale (e.g. continental or global) there are few data sets with a fine grain resolution in meters, these are usually in kilometres or even degrees of latitude and longitude (e.g. Zulian et al. 2013). Even when the fine-grain resolution data and coverage required is available, the data processing time and computation power required is a limitation. Rega et al. (2018) recognize limitations on data availability for Europe. To create the land cover classification mentioned above, they combined high-resolution maps (25m) of woody (Langanke et al. 2017) and herbaceous vegetation (García-Feced et al. 2015) for the continent and use the Morphological Spatial Pattern Analysis method suggested by Soille and Vogt (2009) to identify binary patterns of segmentation of mutually exclusive spatial categories in these the high-resolution maps. This method obtains categories applying a series of operators originating from mathematical morphology. They classified the natural habitat pixels as linear, edge or areal features (Fig. 5.2). The final resolution adopted for this assessment was 100 m, a high-resolution output considering the scale of the study area.

The use of landscape ecology concepts at a non-landscape scale, like the approach used by Collard et al. (2018) at a plot-scale level, is worth mentioning. Based on spatial configuration metrics —such as proximity, edge length or aggregation— and habitat composition —such as land cover type or vegetal structure—, the models suggested by Jonsson et al. (2014) Collard et al. (2018) and (Rega et al. 2018) reach a similar conclusion: a linear forested habitat maximizes service provision (Fig. 5.1). Like pollination, proximity to cropland and edge effect are determining factors and this has major implications for land management and

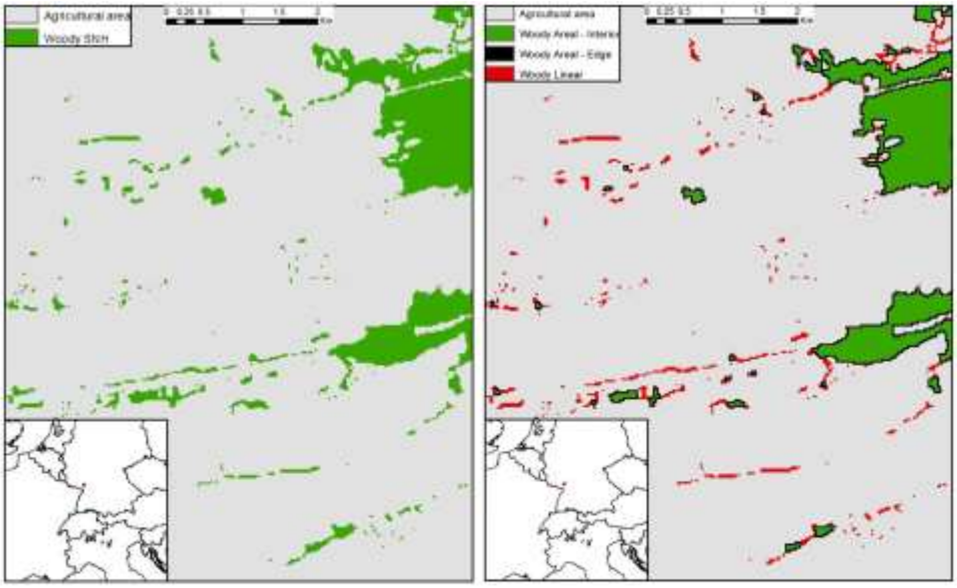


Figure 5.2. Example of the Morphological Spatial Pattern Analysis (Soille and Vogt 2009) on the high-resolution layer of woody seminatural habitat in Europe by Rega et al. (2018). Left: Original map with woody habitat in the agricultural matrix; Right: classification of woody habitat into three mutually exclusive types: woody areal-edge, woody areal-interior and woody linear (resolution= 25m).

conservation strategies. Conservation of natural habitats in agroecosystems is essential to maintain the provision of natural pest control.

Variables suggested in previous models to model natural pest control in the tropics are attainable with current datasets on land cover types (e.g. Arino et al. 2010), forest cover (e.g. Hansen et al. 2013), and climate (e.g. Fick and Hijmans 2017). Although the effect of the resolution of these layers on the model output needs further assessment, the mobility ranges adopted in landscape and continental models (up to 1500 m), suggests that a similar approach to the one adopted for the pantropical pollination model is feasible.

Currently, a 100 m-resolution map of land cover types at global scale provided by the Copernicus Global Land Service (CGLS-100, Tsendbazar et al. 2018) for 2015 is in development. This map provides a map of 20 land cover classes —a similar classification to the GlobCover 2009 map used to model pantropical pollination— that could provide the detail required to model natural pest control at pantropical scale in terms of spatial configuration and vegetations structure. This dataset is already available and shows a higher overall global accuracy (80%, Tsendbazar et al. 2018) than the GlobCover 2009 map (67%, Bontemps et al. 2011). CGLS-100 was developed using 141,000 crowd-sourced training points and validated with 20,000 independent validation points. However, it is still in the 'demonstration' stage, and validation is still in progress.

The use of spatial configuration and land cover type as an indicator of suitability for natural pest control providers in Europe is supported by extensive survey data (Moonen et al. 2016). Although data of comparable magnitude are not available across the tropics, other common approaches like literature- or expert-based knowledge can be used to assess the implementation of similar criteria.

For the studies described above, it is noticeable that when the modelling objective comprises multiple ecosystem services, the variables used are relatively simpler than those used when a single service is modelled (see table 5.1), in this case, natural pest control. The single-service approaches provide a deeper insight into the factors that determine the occurrence and abundance of providers. Especially for natural pest control, the detailed information available on specialised predator-prey/parasitoid-host interactions in agroecosystems (e.g. Jonsson et al. 2014, Wyckhuys et al. 2018) allows a highly detailed modelling approach. But, in a similar way to the single-service vs multiple-service trade-off, a highly specialised model could underestimate the service potential from several providers to several pests. Thus, a generalist approach like the one adopted by Rega et al. (2018) is recommended at pantropical scale.

Based on the current models and the experience gained by modelling pantropical pollination, the selected key provider to model pantropical natural pest control to cropland would be generalist predator/parasitoid insects. As has been done for pollination, data on habitat suitability, mobility range, and activity should be adapted as far as possible to tropical taxa and conditions.

While there is a relatively good understanding of the ecological relationship between populations of natural enemies and the studies described above offer a valuable methodological background to model natural pest control services, it is important to recognize the limited knowledge of the ecological processes that allow the provision of service to agricultural systems. As indicated by the historical failure rate of managed natural pest control (Greathead and Greathead 1992), the relationship between the service provider and natural and modified systems is complex. There is still a great lack of understanding of the mechanisms and key variables that determine the occurrence of this service (Hajek and Eilenberg 2018). To improve the modelling of service provision in the tropics it is necessary to increase the knowledge about the particular conditions required by providers in this area of the world.

The geographic bias in the ecological observations (Martin et al. 2012) and biodiversity studies in modified habitats (Trimble and van Aarde 2012), where European and North American temperate zones are over-represented, limits the understanding of ecological processes in tropical regions, particularly in African and Asian tropical zones (Trimble and van Aarde 2012). This trend reverberates in the understanding of regulating service provision by wild and managed providers (e.g. Bianchi et al. 2006, Potts et al. 2016). Although some studies have shown the relevance of wild natural enemies in tropical agroecosystems (e.g. Drechsler and Settele 2001, Karp and Daily 2014) and there are some cases of success of managed natural pest control of tropical crops (e.g. Nwilene et al. 2008, Myrick et al. 2014), the required information is not yet available on a pantropical scale. As for the pantropical pollination model, a natural pest control model would require tailored sampling at larger scales.

5.3. Animal seed dispersal

Tropical forests are characterised by high alpha diversity of tree species (number of species within a site). Tropical trees tend to grow at a considerable distance from their kind. This characteristic spatial pattern of tropical tree diversity has been explained by the Janzen-Connell theory; observations by Janzen (1970) and Connell (1971) suggest that seedlings have higher probabilities to succeed if they are far from their pest- and pathogen-carrying parents and avoid interspecific competition.

Plants have evolved many methods of seed dispersal, including abiotic dispersal (by wind or water) and biotic dispersal performed by animals. Zoochory (animal transportation) allows long-distance dispersal (>100 m), gene flow, escape from areas of high mortality, colonisation of new sites and dispersal to favourable sites (Wenny et al. 2016). Seed dispersal through fruit ingestion is the primary dispersal mode for over 75% of woody plants in most tropical forest and of 35–56% in other woody ecosystems (Catterall 2018).

5.3.1. Available evidence

Our understanding of the seed dispersal process derives mostly from observation, either by observing dispersion directly or by observing spatial patterns of species occurrence. An experimental approach to study this process is challenging. For instance, altering dispersal by the exclusion of dispersers on the relevant scale —hundreds to thousands of meters in each direction—is hardly achievable (Harrison 2017). Therefore, theoretical models have been a useful resource to understand the process (e.g. Greene and Calogeropoulos 2002). Recently, the loss of providers as a result of anthropogenic activities (see Chapter 2) has allowed a deeper understanding of the process and to test the proposed theories explaining current patterns of species distribution and the effects of provision loss in natural systems.

In brief, long-distance dispersal is expected to increase alpha diversity but reduce beta diversity (the dissimilarity of species composition among sites), i.e. long-distance dispersers promote high species richness and reduce the difference in community structure over large areas. Wandrag et al. (2017) tested this assumption by comparing seedling species richness and spatial distribution in treefall gaps in the isle of Guam, where currently there are no more vertebrate seed dispersers —fully or functionally absent—, with that of neighbouring islands of Saipan and Rota, where dispersers are present and natural systems are practically equal. They showed seed dispersers approximately doubled seedling species richness within canopy gaps and halved species turnover among gaps.

Equally, using the Canary Islands as natural laboratories, Pérez-Méndez et al. (2016) documented a significant reduction of seed dispersal distances along a gradient of human-driven defaunation, with increasing loss of large- and medium-bodied frugivore lizards, which act as seed dispersers. They showed this has an effect on the fine-scale spatial genetic structure of plants. According to their results, the (total or partial) loss of large- and medium-size lizards have resulted in high genetic similarity and smaller effective population sizes of local plant neighbourhoods.

The relationship between frugivores and plants is often referred as diffuse mutualism (e.g. Vander Wall and Longland 2004, Gove et al. 2007), where both plants and dispersers benefit from this interaction and, usually, any focal plant species interacts with a set of potential dispersers and any focal frugivore may potentially disperse several plant species. This is only the case for plant species that are small-seeded (<0.5g), have high annual fecundity, have a sharply peaked fruiting season, and for disperser animals that have a generalised gut and complement their diet with fruits (Howe 1993). There is a specialised relationship between large-seeded plant species with low annual fecundity and extended fruiting season, and dispersers with specialised guts and primarily fruit diet (Fleming et al. 1993, Howe 1993). The richness of disperser species is relevant in cases where plant traits (e.g. seed size) or disperser traits (e.g. gut structure) result in a certain degree of specialist interaction (Pérez-Méndez et al. 2016). However, like pollination and natural pest control, the abundance of providers is key to secure the benefits mentioned above (McConkey and Drake 2006). The abundance of generalist long-distance dispersers, like birds and flying mammals, is essential in forest regeneration (Catterall 2018).

5.3.2. Available spatial models

Early approaches to model seed dispersal spatially are focused on the wind as the main means of dispersal (e.g. Greene and Johnson 1989). And even when some models assume animals as the main dispersal mechanism, this role is assumed as random and the variables considered are based on plant occurrences and seed traits, such as the seed shadow, i.e. the spatial pattern of seed distribution relative to parent trees and other conspecifics (Jordano and Godoy 2002), rather than on service providers (e.g. Pearson and Dawson 2005). However, the need to incorporate animal behaviour has been recognised as necessary to generate realistic spatially explicit models and to improve the understanding of this process (Nathan 2006, Russo et al. 2006).

A combination of field observations and mechanistic models (predicting seed dispersal from the traits of both plant and disperser agents) has been used to incorporate stochasticity and realistic dispersal kernels into seed dispersal models. A dispersal kernel is a 2-dimensional (movement and survival) probability density function describing the probability for a seed to disperse to any position relative to the maternal plant (Klein et al. 2013), incorporating dispersers role into this function can describe a more accurate pattern of seed dispersal. Russo et al. (2006) developed a seed dispersal model at a landscape scale for a tropical tree species by spider monkeys in Peru. They used field-collected data on densities of dispersed (number of freshly defecated seeds in $0.25m^2$) and non-dispersed (non-defecated) seeds, and direct estimates of seed dispersal distances. They showed that dispersal kernels based only on the seed shadow, without incorporating animal contribution, underestimate dispersal variance. They identified shadow heterogeneity and dispersal curve multimodality, i.e. the probability of seed dispersion differs within the mobility range of providers and presents more than one peak (local maximum) in the probability density, showing dispersion occurs mostly at 25m from the parent tree but reaches a second peak at around 175m of the parent plant, which cannot be identified using the seed shadow as only predictor variable (Fig. 5.3a).

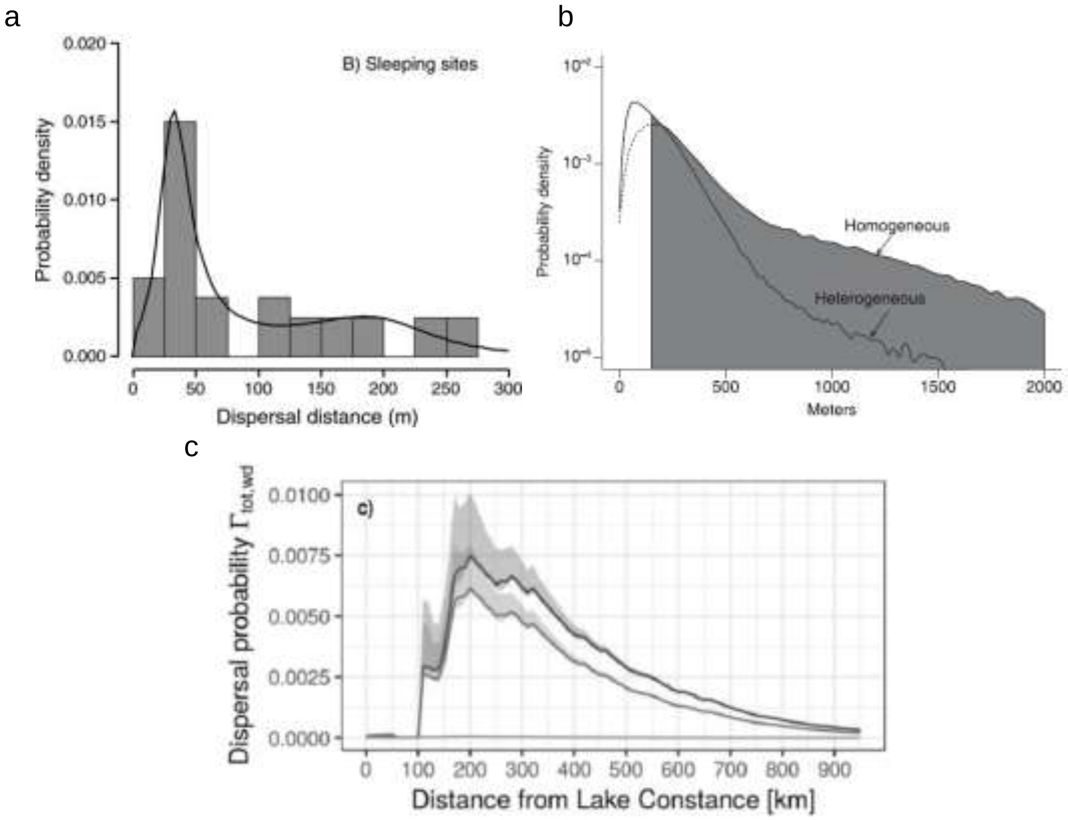


Figure 5.3 Similarities in seed dispersal probability functions. The distributions suggested for seeds dispersed by a) spider monkeys (Russo et al. 2006), b) bluebirds (Levey et al. 2008) and c) mallards (Kleyheeg et al. 2019) are characterised by initial low probabilities, followed by a peak and a gradual decrease. This explained by the time between consumption and defecation of seeds.

Also based on field-collected data, Levey et al. (2005, 2008) generated a seed dispersal model at the landscape scale for temperate forests seeds by bluebirds in the eastern United States. They used empirical measures of perching time, length of movement and direction of movement to simulate movements of a bluebird and assess the effects of natural habitat corridors on seed dispersal. The dispersal pattern was defined by edge-driven behaviour, bluebirds prefer to stay in matrix habitat as they move between habitat patches.

Recently, a broad-scale model was suggested by Kleyheeg et al. (2019) to assess the service provided by migratory mallards to wetland regeneration in Europe. Here, seed dispersal is explicitly recognised as a service, not only as an ecosystem process. Wetland regeneration through seed dispersal provides natural water quality improvement, flood protection, shoreline erosion control, opportunities for recreation among many other ecosystem services (Clarkson et al. 2013). Mallards are granivores, they consume the seeds of over 300 European plant species, part of the seeds they ingest remain viable after digestion. They used GPS tracking data of 51 individuals to model seed dispersal. Seed release was strongly influenced by fasting before migration, offering minimal or null probability for seed dispersal between departure and first stopover and reaching a maximum around 300-400 km (Fig. 5.3c). This model was designed to be highly replicable to other disperser species and ecosystems. However, the limitations of the availability of tracking data are recognised.

Effect of landscape structure

Along with the role of biotic dispersers in spatial models, the role of landscape structure has been assessed. Pearson and Dawson (2005) developed a mechanistic model to assess the relevance of strategic planning of conservation areas under climate change. The model suggests that the relative importance of landscape structure in determining plant migration ability may decrease as the potential for long-distance dispersal increases, i.e. the fragmented natural habitats would be as (un)suitable for seed dispersion as clumped or connected areas when facing climate change. However, this model does not assess animal response to fragmentation, even when animals are the assumed dispersal agent.

In contrast, Levey et al. (2008) include the response of dispersers to different configurations of deforested patches. The model predicts that non-forested patches with corridors or other narrow extensions receive higher numbers of seeds than patches without corridors or extensions. Dispersal distances are generally shorter in heterogeneous landscapes than in homogeneous landscapes (Fig. 5.3b), suggesting that patches divert the movement of seed dispersers, which increases the probability of seed defecation in the patches. Dispersal kernels for seeds in homogeneous landscapes were smooth and with long tails, whereas those in heterogeneous landscapes were irregular (Fig. 5.3b). This difference may be caused by dispersers being attracted to patches and spending more time in them than in matrix, thereby reducing the distance seeds are dispersed.

5.3.3. Modelling pantropical seed dispersal

Habitat sufficiency and disperser mobility are determinants of the seed dispersal service. However, unlike for pollination and pest control services, the relationship between habitat structure and seed dispersers is not yet clearly identified (Catterall 2018). Equally, the probability of service provision as a function of distance seems more complex than that suggested for insect pollinators, where an exponential decrease is described (see section 3.2.1.2, Fig. 5.3).

Despite the challenge that the nature of this process signifies, the studies described above show it is possible to obtain a model at the landscape and European scales for specific providers. Nevertheless, the level of accuracy is given by the detailed information required to feed these models. Since knowledge for several species and data availability is an important limitation at broad scales, and particularly in the tropics, there is a need to assess other possible indicators for seed dispersal provision.

Seed dispersal indicators

Currently, public collaborative databases (e.g. Global Biodiversity Information Facility, GBIF; Integrated Digitized Biocollections, iDigBio; Botanical Information and Ecology Network, BIEN) represent a valuable source of information on global biodiversity. Although the datasets compiled are not exempt from geographical, temporal or taxonomic bias (James et al. 2018), they facilitate analyses that can improve our understanding of natural processes at broad scales (e.g. Pinto-Ledezma et al. 2018). Along with data availability, the identification of the best approach and ability to analyse the data are essential to understand the underlying mechanisms of service provision.

Among the best-represented taxonomic groups in these databases are birds and mammals (Troudet et al. 2017). Information on distribution, abundance, and population changes through time and space of frugivore species are highly relevant indicators of potential service provision. As the evidence suggests, extinction or reduction of disperser population can have a negative effect on plant community structure. The availability of historical records can be an important source of information on the potential distribution of service loss, although temporal bias in the records should be considered.

Along with daily dispersal patterns, like the ones described above, it is important to include seasonal migration into ecosystem service modelling. Frugivore populations in tropical forests have very dynamic distributions, they move over large areas to follow temporal and spatial changes in food resources (Loiselle and Blake 1992). These populations tend to perform seasonal altitudinal migrations. For this, spatiotemporal information provided in public databases is essential (i.e. geographic coordinates and collection/observation date).

Unlike temperate forest, where seasonality is mostly determined by temperature, tropical forest phenology varies in response to other environmental conditions and specific adaptation. In the case of tropical dry forests, seasonality is mostly determined by precipitation, with marked dry and wet seasons. In tropical moist forests, where there is no marked dry season, foliar development (production, senescence, and longevity) is largely under adaptative species-specific physiological control rather than environmental control (Reich 1995). While precipitation and net primary productivity can be used as indicators of seasonality in tropical dry forests and moist forests, respectively, fruit production tends to be staggered throughout the year, reflecting the high variation in development time and loss of fruits among species (Girardin et al. 2016). Variation in frugivore abundance can be used as an indicator of spatiotemporal patterns fruit of production.

Record of seedlings occurrence can also be useful, as shown in the Guam Island study (Wandrag et al. 2017). At the landscape scale, beta diversity patterns showed to be an effective indicator of seed dispersal function. However, at a broad scale, these are also a result of historical processes, such as geographical isolation or environmental variation (Pinto-Ledezma et al. 2018). Since ecological and historical processes are not mutually exclusive, there is potential to upscale this indicator. However, the occurrence of both events must be considered by analyses. Along with spatiotemporal information, records of plant species specimen traits (e.g. maximum longevity, height, fruiting) can provide information on service occurrence.

At this stage, high curatorial effort, spatial data processing and a vast improvement of the underlying ecological mechanisms determining animal seed dispersal are required to obtain useful information from available datasets. However, the development of seed dispersal indicators is imperative to advance methods and techniques that allow accurate monitoring of the process in tropical forest and thus improve management and conservation.

5.4. A pantropical faunal ecosystem service model

The approaches adopted to model natural pest control and seed dispersal are diverse and involve a varied synthesis of theoretical and empirical knowledge (e.g. Rega et al. 2018, Kleyheeg et al. 2019). However, it is possible to recognise habitat suitability and mobility of providers as the common features to model the addressed FES, including pollination. Regardless of the level of detail added to increase the accuracy when modelled independently, these variables must be considered if a multi-service spatial model is the aim.

Pollination and natural pest control

The resemblance between pollination and natural pest control providers, as long as both are insect populations, facilitates the development of a multi-FES model. First, the evidence available on the positive relationship between natural habitat and the abundance of providers for both services can be integrated. The scoring of land cover types based on suitability for providers can be weighed independently for both target providers.

Second, a similar approach can be used to incorporate a mobility variable, i.e. flight distance. For both provisions a maximum distance can be set based on current evidence — 1500 m is suggested as a maximum relevant distance— and a distance-weighted function can be adapted for both providers. While the pantropical pollination model suggests an exponential decay function (section 3.2.1.2), the pan-European model opts for a half-bell shaped distribution (Rega et al. 2018). Both functions suggest a decrease in service from the target cell (i.e. cell designated as a nesting site of providers) towards surrounding cells, therefore an 'intermediate' function between an exponential decay and a half-bell shaped function could be a function determining a distinctive peak in the target cell followed by a steep decline and heavy tails as the distance from target cell increases.

Third, as explained for pollination, ambient temperature strongly influence insect performance by imposing limits on reproduction, growth and activity (MacMillan and Sinclair 2011), and consequently, in service provision. The foraging activity variable suggested for pollinators (see Chapter 3), can be modified to include physiological limits known for generalist predators/parasitoids. Bees show a positive linear relationship between activity and temperatures above 10°C (Corbet et al. 1993), with a maximum limit observed in tropical wild bees of 37°C, after which mortality rates increases (Macías-Macías et al. 2011). The optimal temperature range reported for some tropical parasitoids is 26-32°C (Kroder et al. 2006).

It is possible to adopt a common threshold for providers, keeping in mind that this would imply a generalisation of the optimal temperature range, and would not capture the different responses of individual species to climate (e.g. Stone 1993, Macías-Macías et al. 2011). Alternatively, independent activity variables can be calculated, and each cell could increase or decrease its suitability depending on the activity predicted for a single, or both services. The first option would represent a simpler modelling approach. However, it could underestimate pollination provision. On the other hand, the second option could provide a more accurate estimate of provision for both services, but it could increase model complexity and, along with it, the uncertainty (Snowling and Kramer 2001).

Insect-provided services vs long-distance seed dispersal service

The approaches to model long-distance seed dispersal show significant differences to pollination or natural pest control. While the occurrence of natural habitats is beneficial for all FES providers, the process of provision contrasts highly in the spatial dimension. First, the scale at which the process occurs is greater for seed dispersal (usually thousands of meters), allowing a coarser grain of resolution for seed dispersal assessment.

Second, unlike pollination or natural pest control —where the probability of service provision decreases with distance—, seed dispersal shows a more complex relationship with distance. The probability of seed release (i.e. defecation) increases with distance initially, as it takes time for the digestion to occur. Then the probability of release decreases gradually, like a right-skewed Gaussian distribution (Fig. 5.3). Furthermore, this function can be multimodal (several peaks), especially if migratory species are considered, as providers can disperse (defecate) seeds at different distances, due to digestion times and home-range and migratory movements.

Third, while a heterogeneous landscape, i.e. combining natural habitat and cropland, is recognised as highly beneficial for pollination and natural pest control (e.g. Rega et al. 2018), little is known regarding the potential effects of landscape heterogeneity on spatial patterns of long-distance seed dispersal (Levey et al. 2008). While the challenges related to the assessment of this ecosystem process persist, development of novel field techniques, data collection methods, and modelling approaches (e.g. Kleyheeg et al. 2019) increase the knowledge on the landscape-disperser relationship.

Finally, whilst seed dispersers provide the benefit of regenerating of natural systems (e.g. forest, Hougner et al. 2006, wetlands, Kleyheeg et al. 2019), which contributes directly to human-wellbeing (e.g. flood protection, water quality regulation, recreation), animal seed dispersal usually is not beneficial to cropland (e.g. frugivore mammals and birds, Naughton-Treves and Treves 2005). Most of the evidence suggests seed dispersal is highly beneficial for natural systems and, in contrast to pollination and natural pest control, the spatial overlap of frugivores and cropland distributions can result in disservice provision if crops are foraged by frugivorous (Gutierrez-Arellano and Mulligan 2018). Therefore, distance has an equally relevant but opposite relationship on service provision to agroecosystems. In this case, the distinction between potential and realised provision is given by forest distribution.

5.5. Conclusions

Given the current data availability, a model that incorporates pollination and natural pest control at pantropical scale is achievable in terms of the methodological approach. However, the limited ecological understanding of service provision and data availability at large scale in tropical zones requires a much more complete dataset. Equally, a sensitivity and validation analyses would still be required for natural pest control service model. This would be relevant to gain a better understanding of ecological processes underpinning the service globally and to improve agricultural planning in tropical areas.

Regarding modelling the seed dispersal service, current data and methodological limitations prevent the generation of an accurate model at the pantropical scale. The evidence available allows the identification of patterns of animal behaviour influencing service provision, such as general probability distribution of seed release as a function of distance. However, further development of indicators, methods and techniques are required to incorporate this service to other ES models.

The similarities between pollination and natural pest control processes, and the difference between these and seed dispersal, exemplify the incidence of synergies and trade-offs when a bundle of services is assessed. Although the demand of agriculture-related regulation services is expected to increase in the tropics (Mulligan 2015b, Gutierrez-Arellano and Mulligan 2018), a purely agriculture-related approach to manage and conserve FES would be detrimental for other ES and biodiversity.

Pollination, natural pest control and seed dispersal are just a few of the many regulating services provided by fauna which are beneficial for agro- and natural systems, such as waste decomposition (Luck et al. 2009) or water regulation through biogenic structures (Lavelle et al. 2006), disturbance prevention (Paoli et al. 2017). These services are barely recognized and are scarcely understood (Lavelle et al. 2006). The recognition and study of faunal ecosystem services across different systems and biomes would improve the conservation of actors and processes that contribute to the provision of regulating services. The inclusion of these services would contribute to a more comprehensive assessment of bundles of services and their relationship with biodiversity.

Modelling multiple ecosystem services at broad scales can provide an integrative perspective to inform conservation and management decisions of tropical forests. Strategic conservation of natural habitats along with planning for sustainable agriculture is recommended to maximise FES provision while reducing pressure on biodiversity and natural systems. This chapter has provided a blueprint for a model that incorporates pollination and natural pest control at pantropical scale, which may be useful in extending the pollination model developed in this thesis.

6 Conclusions and future work

Ecosystem functions can provide services to humans directly or indirectly. The distinction between direct or indirect service is linked to human perception, while direct provision is perceived as a benefit, indirect provision is unperceived (or poorly perceived) as a such (Costanza et al. 2017, Potschin and Haines-Young 2017). While a direct benefit can be recognised in some regulating services provided by fauna, such as pollination and natural pest control, there are many cases where the intervention of fauna occurs in an early stage in the cascade of processes that lead other ecosystem functions or final benefits (Potschin and Haines-Young 2017). For instance, seed dispersers contribute to vegetation regeneration, which in turn will provide other services, such as soil erosion regulation or provisioning of raw materials.

As all components of ecosystems, ecosystem services are intrinsically linked together. However, the definition and categorisation of services enable their assessment, modelling, and valuation (Costanza et al. 2017).To better understand the complex pathways to ecosystem service delivery, it is imperative to recognise the different actors involved. Thus, the suggested concept of faunal ecosystem services aims to recognise and advance the research on the role of fauna in the intricate ecological processes which ultimately contribute to human well-being.

Due to the highly complex interactions of fauna with natural systems and the delivery of ecosystem services, it is recognised that the categorisation of these services cannot be strict. However, the faunal ecosystem service concept contributes to the characterisation of services, which is essential for their management and conservation.

The first objective of this study was achieved through the scoping review presented in Chapter 2. This review allowed the identification of some of the regulating services that are provided by fauna: pollination, natural pest control, natural disease control and seed dispersal. Pollination, by wild bees and other wild pollinator insects, and natural pest control, by predators and parasitoids of invertebrate pests, are especially important for agriculture. These regulation processes can simultaneously provide disservices, including invasive species and species pest outbreaks. Evidence suggests that the abundance of beneficial providers is a key trait of biodiversity for the occurrence of service. However, richness is equally relevant depending on the level of specialisation of ecological interactions required for service provision (e.g. specialised plant-pollinator or plant-seed disperser interactions). Along with abundance, richness other measures of biodiversity must be considered to explore the relationship between biodiversity and ecosystem services.

The recognition of land use and cover change (LUCC) as one of the main threats to biodiversity and ES has increased the interest in understanding the relationship between biodiversity and ES provision and the effects of LUCC on it. Agricultural expansion is currently one of the main causes of LUCC in tropical forests. The review allowed the identification of landscape homogenisation, habitat loss, habitat fragmentation and microclimatic changes as the main consequences of agriculturalisation with negative impacts on providers abundance, and as a result, on ecosystem service provision. The review answered the first question: 'Does habitat loss and degradation due to land-use conversion from forest to cropland have an impact on FES provision?' Habitat loss and habitat degradation due to agriculturalisation have a negative impact on FES provision due to the loss of richness and, especially, the abundance of providers (Gutierrez-Arellano and Mulligan 2018).

Spatially explicit ES models are valuable tools to assess synergies and trade-offs among ES and between ES provision and biodiversity. They assist in obtaining robust and location-specific results to inform management and conservation strategies. Regulating FES are the most relevant biodiversity-related services for agriculture and are intrinsically linked to the conservation of natural ecosystems. Currently, biodiversity conservation and regulating services for agriculture are of utmost priority in the tropical forests, due to the growing demand for food production globally and the increasing pressure this signifies for tropical ecosystems.

The second objective of this thesis: ‘To generate a pantropical spatial distribution model of a faunal ecosystem service provision and demand’ was fulfilled in Chapter 3. Building on previously suggested models, using empirical data for tropical providers and including novel variables and methods to improve the estimation of providers abundance, it was possible to generate a pantropical spatial pollination model (section 3.2.1.2). This model distinguishes service provision, i.e. potential pollination, from overlap with service demand, i.e. realised pollination. This distinction is relevant to identify current benefits for tropical crops, but also to assess the potential benefit in the future (as both provision and demand will change with LUCC) and/or its interaction with other ecosystem services and biodiversity.

The conservation of wild pollinators is essential to compensate and possibly reduce the detrimental effects of managed pollinators in natural systems. The development of a pantropical spatial model of pollination allowed the assessment of the current status of protection of the service provided by wild bees to tropical crops. The potential pollination models suggested that over three-quarters of protected areas can contribute to tropical crop pollination. Considering current demand of service, small-sized protected areas provide higher pollination service than large ones as a result of their greater proximity to crops and their greater perimeter per unit area (i.e. with more pollinators in proximity to crops). This type of analysis facilitates the identification of the different contributions of protected areas to ES provision in general.

Protection of varying-size forest areas provides different outcomes, all equally relevant for ecosystem service and biodiversity conservation. Larger-sized protected areas tend to harbour a larger number of species and viable populations, provide habitat to medium- or large-sized fauna, which can provide other FES (e.g. seed dispersal) and are relevant for the provision of other ES (e.g. carbon sequestration). On the other hand, smaller-sized protected areas tend to provide habitat for small-sized fauna and tend to be closer to human-modified habitats (e.g. cropland) facilitating the provision of ES where proximity is a determinant factor (e.g. pollination and natural pest control) and are also under higher anthropogenic pressure. Therefore, it is suggested to consider pollination service alongside other ES in protected area management decisions.

The pollination model suggested in Chapter 3 proposes a more accurate representation of the effect of distance from nesting sites on pollination provision than the suggested by the InVEST model (Tallis et al. 2011). This widely used model uses a mean distance value to represent service provision (e.g. 2 km, Chaplin-Kramer et al. 2019), assuming a uniform distribution of service within this distance. However, the exponential decrease in foraging activity as the distance from the nest increases is well recognised in pollinating bees (Abrol 1988, Gathmann and Tscharntke 2002, Zurbuchen et al. 2010). Thus, the exponential decay function reflects a higher provision of service near the nest. While this function can be improved using a bigger sample of tropical species, this is a valuable contribution to the theoretical representation of the process.

Currently, the pollination model suggested in this thesis requires to increase the sample of species used to estimate the foraging distance variable. The model must be validated and the hypothesis that landscapes predicted as wild-bee scarce have crop pollination deficit must be tested. Equally, the model does not consider population dynamics over time, the effects of climate change on pollinators, the negative effect of pesticides on pollinator abundance and the role of species richness. There is a large scope for improvement. However, this improvement is constrained by the current lack of data. The knowledge about the current status of diversity and abundance of wild pollinators, as well as the effects of land conversion on service provision at broad scales, is biased to temperate zones (Europe and North America). It is imperative to increase the knowledge and data availability in tropical zones to provide more accurate projections of providers and service status facing the pressures of global change.

Chapter 4 accomplishes objective 3: ‘To generate projections of land use and cover change from forest to cropland at pantropical scale’; and objective 4: ‘To quantify changes in FES supply and demand due to land-use change under different scenarios of conversion’. LUCC spatial models are useful tools to understand the causes and consequences of this process at specific locations. Currently, few models have a global scope, one of them is QUICKLUC. This model allowed the generation of projections of future deforestation and conversion to cropland pantropically. Thanks to the integration of spatially explicit FES and LUCC models, it was possible to understand how scenarios for agriculturalisation can affect the distribution of FES provision in the future (section 4.2.3), answering the second research question: ‘How does agriculturalisation affect the distribution of FES provision and demand in and near tropical forests?’.

The assessment of LUCC effects on the pollination service at regional scale allowed first, to apply the model at a smaller spatial scale before their application at pantropical scale, and secondly, to identify variation among sites with diverse patterns and trends of landscape, land use, service provision and LUCC. Different percentage and distribution of current forest cover, the proportion of mosaic (vegetation-cropland) area and different deforestation rates, produce mixed effects on pollination provision (section 4.3.2).

Chapter 4, solves the final research question: ‘What are the possible impacts on FES supply and demand under different scenarios of land-use change from forest to cropland in the tropics?’ Projections suggested an increase of pollination service with LUCC in some regions in the short term, indicating that they have not reached their maximum in realised service yet. These results are not intended to encourage agriculturalisation, but to show how these projections are useful to understand patterns and trends of service provision. Thus, to estimate where and when an inflexion point could be reached, and to assess the role of protected forest in this process. In general, across all ES the more demand for the service the greater the service provided so LUCC generally increases service provision until the ecosystem that provides the service is itself undermined by LUCC (Mulligan 2015b).

In general, forest loss resulting from increased cropland area has a negative impact on pollination service pantropically in the long term. This could be ameliorated by the effectiveness of current protected areas. However, a decrease in deforestation rates, an increase in forest protection and incorporation of natural habitats in agricultural landscapes are necessary to maintain current pollination service through time.

Further assessment on the relationship between fragmentation and change in service provision, along with the consideration of other fragmentation patterns derived from alternative scenarios of change is recommended. Equally, the scope of this research did not include an assessment of the effects of climate change or LUCC other than agriculturalisation on pollinator abundance. However, given their relevance in environmental global change, the incorporation of these factors in the proposed models and scenarios is suggested.

It is important to take into account the assumptions made to produce the scenarios as well as the limitations of the model. The undifferentiated tree cover of natural habitats and forest plantations can produce an overestimation of pollination service due to the designation of equal nesting and foraging suitability for wild pollinators. Equally, the analysis only assessed the effect of agriculturalisation on service provision and no other transition was included in the model, further assessment of other LUCC processes is still required. Also, the effectiveness of protected areas is highly variable in time and space, it is recommended to consider other effectiveness indexes to explore different scenarios of management in different regions across the study area. Additionally, deforestation rates were assumed constant in the long term, an unlikely situation given the several factors that could influence LUCC processes in the future. Thus, the results obtained must be interpreted under the assumptions made to generate the projected deforestation scenarios and, depending on the context of time and space of interest, further exploration and adaptation of the parameters used are recommended.

The assessment of the effects of agriculturalisation on pollination services presented in this thesis had some limitations that could be overcome with greater data availability and computing power. First, increasing the information on current suitability zones and potential distribution of pollinator-dependent crops in the future, as currently available for some major crops, would provide a more accurate projection of future realised pollination service. Second, a wide-scale high-resolution analysis can be achieved if the computing time and infrastructure are available, to provide a spatially detailed projection of change at pantropical scale. As well as discussing the possible approaches and challenges to model natural pest control and seed dispersal, Chapter 5 highlights the importance of considering several FES to enhance synergies and understand trade-offs. Given the similarities between pollination and natural pest control providers (in terms of relationship with habitat structure, mobility and spatial patterns of service provision) natural pest control shows a great potential to be spatially modelled at pantropical scales, to be integrated to the suggested pollination model as long as the ecological knowledge and data availability for tropical regions improves. For seed dispersal, there is still much to do to determine the best indicators of provider abundance and its relationship with habitat structure.

The recognition level of pollination and, to a lesser extent, natural pest control as ecosystem services provided by fauna is disproportionally higher compared to the many faunal regulating services of which little is known and whose processes are poorly understood. The review presented in Chapter 5 provides a glance to the complexity involved in the spatial modelling of ecosystem services and the relevance of ecological knowledge and data availability to provide an accurate representation of service provision. The recognition of providers and the understanding of processes underpinning regulating services is imperative to carry out comprehensive assessments of ecosystem services and their relationship with biodiversity to inform management and conservation decisions. Although much work is yet to be done to improve the approaches to model faunal ecosystem services spatially and to include other causes of environmental change, this study fulfilled its key objectives. First, to gather the evidence that shows the relevance of fauna on the provision of regulating services at different geographical scales and identify those of importance for tropical agriculture. Second to develop an initial approach to model a faunal ecosystem service, pollination by wild bees, at pantropical scale. Third, to assess the possible effects of agriculturalisation on pollination provision. Finally, to assess the opportunity to integrate multiple faunal ecosystem services and to consider them in conservation and management decisions. This study suggests that enhancement of the faunal ecosystem services, pollination and natural pest control, can have positive effects on agroecosystems by increasing productivity and food security, and on natural systems by reducing the pressure of agriculturalisation on both, provider and non-provider populations. An initial assessment indicates this can be negatively affected by unsustainable agriculturalisation. Finally, this study showed how spatial models are a powerful tool to identify distribution patterns of ecosystem services and to inform management decisions to conserve ecosystem services and biodiversity in the tropical forest.

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Appendices

Appendix A.Sensitivity analysis of a pantropical model of pollination

A series of sensitivity analyses were carried out to understand how changes in the variables used in the pantropical pollination model described in Chapter 3 (section 3.2.1.2) can affect the output of the model, i.e. pollination index. The variables assessed were nesting suitability, foraging suitability, slope for nesting preferences, slope for foraging preferences, foraging distance, probability of movement, foraging activity and density of barriers.

First, to avoid including redundant variables (i.e. the information provided by a variable is already provided by another variable) a correlation analysis was carried out. Second, to assess the interaction and relative importance of these variables a linear regression analysis was performed using a backward selection method. With this method, the model includes the minimum amount of variables while maximizing its explanatory power, thus is possible to identify which interacting variables best explain the model and which ones can be excluded.

Finally, the influence of the change in variables on the spatial configuration of the potential pollination model output was assessed in a sample site (Amazon region) of the study area. A comparative spatial analysis was carried out after applying a one-at-a-time variation method, in which the values of one variable are changed, the model is re-run and the output is compared to the original output.

Methods

Correlation analysis

To assess the relationship between inputs and to avoid redundancy in the model it was carried out a correlation analysis. A simple random sampling was performed to obtain the values of each of the assessed variables and the final pollination maps from 10,000 pixels across the study area. Thus, each pixel has a value associated to each of the variables (i.e. nesting suitability, foraging suitability, slope for nesting, slope for foraging, likelihood of movement, foraging distance, foraging activity and density of barriers.

First, a normality test of these 10,000 values was performed per variable. A Spearman correlation analysis was selected since the variables were not normally distributed (Fig. A.1). The Spearman correlation analyses performed between pairs of continuous variables (i.e. nesting suitability, foraging suitability, likelihood of movement, foraging distance, foraging activity and density of barriers). Despite being numerical, the slope variables (for nesting and foraging) showed a categorical distribution (Fig. A.1c, d), i.e. instead of a continuous variable, it showed only two possible values (nesting = 1 or 0.6, foraging= 1 or 0.2). Therefore, these were treated as categorical variables. Their effect on the other variables was assessed performing a Mann-Whitney test. The nesting for slope variable was used as a grouping variable, forming two groups (1 and 0.6) for the values of each of the continuous variables. The two groups of each variable were compared to test if there is a significant difference between them. A significant difference would indicate a correlation between the slope for nesting variable and the continuous variable assessed. This procedure was repeated for the slope for foraging variable. All the statistical analysis were performed using SPSS 24(IBM, 2016).

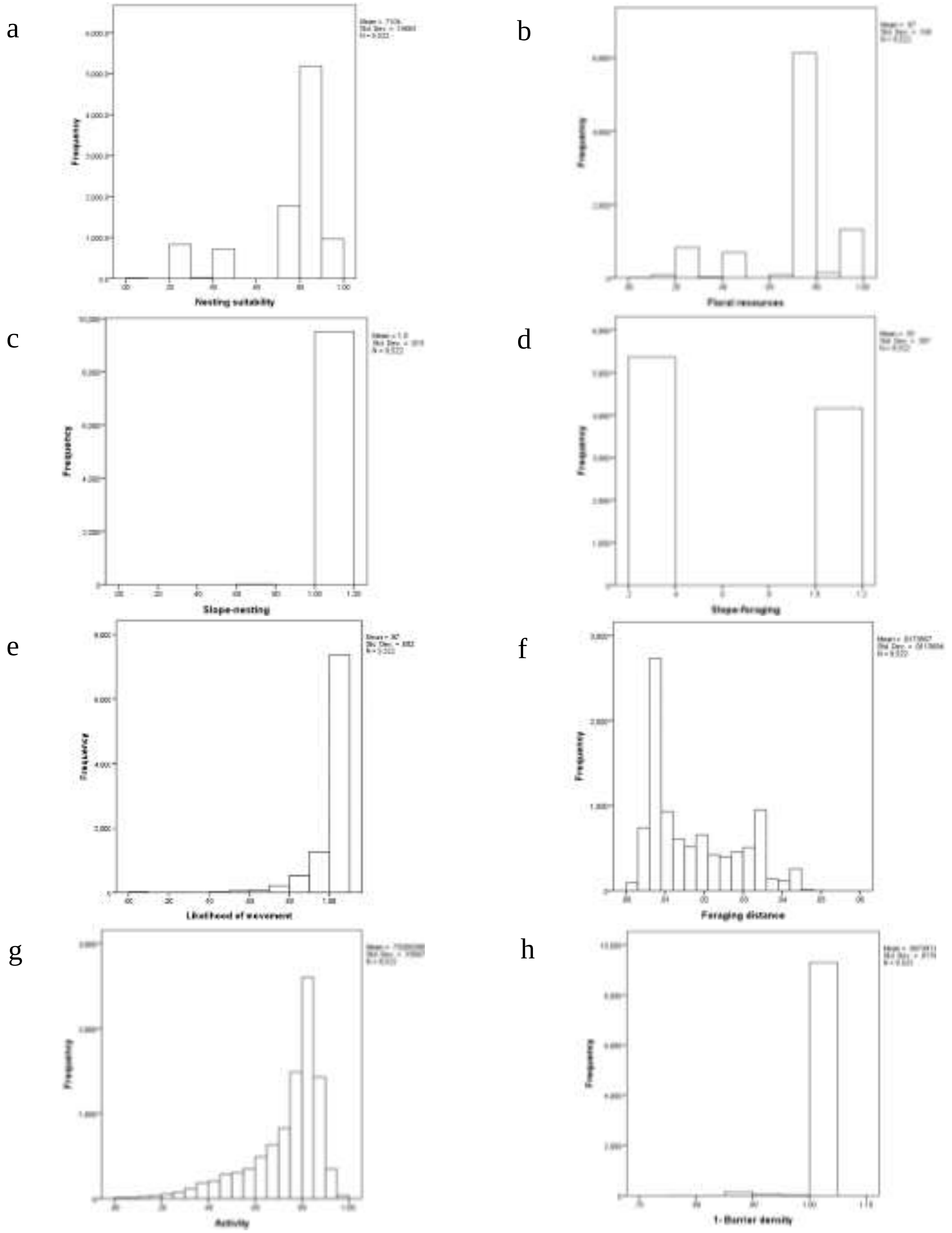


Figure A.1. Distribution of values of the variables used for the potential pollination model obtained from 10,000 randomly selected pixels throughout the study area: a) nesting suitability, b) foraging suitability, c) slope for nesting, d) slope for foraging, e) likelihood of movement, f) Foraging distance, g) foraging activity and h) density of barriers.

Linear regression

A linear regression analysis was used to assess the relevance of each variable for the model. A backward selection method was used to obtain the smallest set that significantly predicted the response variable, i.e. potential pollination. With this method, initially, all variables are entered into the model and then eliminated one by one to leave only significant predictor variables. An *a posteriori* assessment of the distribution of the residuals was made to confirm that the distribution of the response variable given the distribution of the predictor variables meets the assumptions to perform a regression analysis.

One-at-a-time variation of model inputs

To assess the influence of the variability of the variables on the spatial configuration of pollination index values, a one-at-a-time analysis was performed followed by a per-pixel comparison among the original output map and the resultant output maps generated with modified variables. First, each input was systematically varied at a time while the others remain fixed. Each input was increased or decreased by a factor of their respective standard deviation, up to ±4 standard deviations to include 100% of the values present in the distribution (Downing et al., 1985). By using the standard deviation as a varying factor instead of a percentage of the input, this sensitivity measure takes into account the parameter's variability and the associated influence on model output (Hamby, 1994).

Given the processing time required to run the potential pollination model, the one-at-a-time variation analysis was performed in a sample site (Fig. A.2). First, the standard deviation of each variable in this site was estimated by randomly selecting 1000 pixels (Table A.1). Then, a variable layer was modified by adding the value of one standard deviation (e.g. nesting suitability, +0.2201) and the model was run again. Next, this same variable was modified by adding the values of two standard deviations (e.g. nesting suitability, +0.4402) and the model was run again. This was repeated up to adding the value of four standard deviations and then subtracting up to 4 standard deviations to the variable layer. Thus, after modifying a variable, eight different output maps were obtained. This was done for each of the continuous variables.

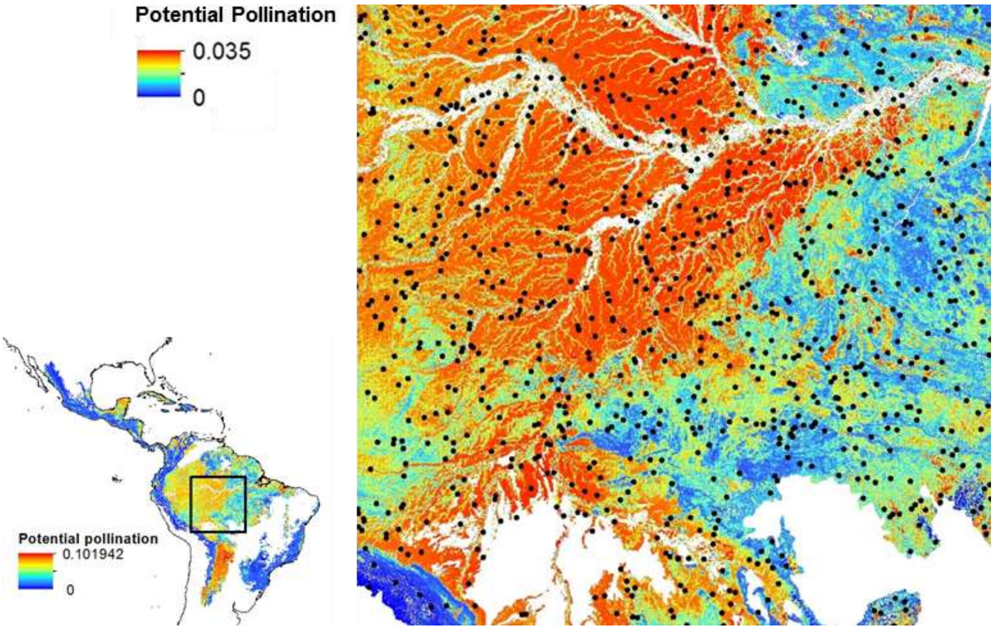


Figure A.2. Sample site of the study area selected to perform the one-at-a-time variation analysis. The Amazon region was selected as a sample site where 1000 pixels were randomly selected (•) to obtain the values of the variables used in the pollination model associated to each pixel, these values were then used to carry out the one-at-a-time variation analysis.

Table A.1. Mean and standard deviation of the sample (N=1000) of the output (*) and the variables used in the potential pollination model.

	Mean	Standard deviation
Potential pollination*	0.0134	0.0082
Nesting suitability	0.7301	0.2201
Foraging suitability	0.6631	0.1661
Likelihood of movement	0.9139	0.2655
Foraging distance	0.0232	0.0098
Foraging activity	0.8201	0.0600
Barrier density	0.9993	0.0090

Finally, a comparison between the original output map and each of the eight output maps obtained after the variation of each variable was performed using the software Map Comparison Kit 3.3 (Visser and Nijs, 2006). The software calculates a Fuzzy numerical statistic (s), where the formula

$$s\ (a,b) = 1 - \frac{|a-b|}{\max\ (|a|,|b|)} \tag{1}$$

is applied to find the similarity of two values (a and b). This statistics indicates the overall similarity between the maps, where 1 is complete similarity and 0 complete dissimilarity. Also, it is created a map per comparison showing the spatial extent of similarity between the maps on a per-pixel basis.

Results

Correlation analysis

The Spearman correlation showed a weak significant correlation between continuous variables nesting suitability, foraging suitability, likelihood of movement, foraging distance, foraging activity, and density of barriers ($R<0.23$, $p\leq 0.01$) except between activity and distance, which showed a moderate-significant correlation ($R=0.52$, $p\leq 0.01$, Table A.2). Regarding the effect of categorical variables on continuous variables assessed with the Mann-Whitney test, the input slope for nesting showed a significant effect on the variables nesting suitability, foraging activity and distance ($p<0.01$). The slope for foraging showed a significant effect on all the inputs ($p<0.01$). These results indicate a correlation between the slope variables and the continuous variables.

Table A.2. Correlation coefficients between continuous variables: nesting suitability (N), foraging suitability (F), likelihood of movement (M), foraging distance (D), foraging activity (A), and density of barriers (B).

	N	F	M	D	B	A
N	1.000					
F	.388**	1.000				
M	-.169**	-.221**	1.000			
D	.094**	.225**	.073**	1.000		
B	-.070**	-.125**	0.018	-.037**	1.000	
A	-.169**	-.090**	.050**	.522**	-0.020	1.000

** Correlation is significant at the 0.01 level (2-tailed).

Linear regression

The regression analysis generated two models using the backward selection method, which involved the generation of a first model including all variables and a second model including fewer variables(Table A.3). The first model showed a significant relationship between the response variable (potential pollination) and all the variable except slope for nesting ($\alpha=0.05$, $p=0.106$). The backward selection excluded this variable for the second model excluded this variable. Both models were equally fit (adjusted $R^2= 0.941$, $p<0.01$), showing that slope for nesting is not an informative variable. According to the backward selection method, the second model was the best because it was equally fit with fewer variables.The fact that no more models were generated (i.e. no more variables were eliminated) indicates that the rest of the variables have a significant relationship with the response variable and the removal of any of these would decrease the fit of the model.

Regarding the relevance of the inputs, it was used the beta coefficients to assess the relative strength of the predictor variables, foraging distance (D) was the most important variable, followed by nesting suitability (N), while least important was slope for foraging (Fs; Table A.3).

Table A.3. Linear regression analysis for the response variable potential pollination (PP) using the backward selection method and the predictor variables: foraging distance (D), nesting suitability (N), foraging activity (A), foraging suitability (F), density of barriers (B), likelihood of movement (M), slope for foraging preferences (Fs), and slope for nesting preferences (Ns). It is shown the beta coefficient, estimated standard error in brackets, and t score per variable, and the adjusted R^2 per model.

	Model 1		Model 2[a]	
	β	t	β	t
(Constant)	-0.025 (0.0017)	-14.592**	-0.023 (0.0011)	-20.130**
D	0.644 (0.0035)	182.390**	0.644 (0.0035)	182.410**
N	0.011 (0.0001)	75.329**	0.011 (0.0001)	75.315**
A	0.006 (0.0001)	42.841**	0.006 (0.0001)	43.025**
F	-0.004 (0.0002)	-28.097**	-0.004 (0.0002)	-28.117**
B	0.008 (0.0011)	7.302**	0.008 (0.0011)	7.291**
M	0.005 (0.0002)	21.151**	0.005 (0.0002)	21.146**
Fs	-0.002 (0.0001)	-19.052**	-0.002 (0.0001)	-19.069**
Ns	0.002 (0.0013)	1.616	—	—
R^2	0.941		0.941	

Dependent variable: PP
** Significant at the 0.01 level (2-tailed).
[a] Best model

One-at-a- time variation of model inputs

When modifying the variables nesting suitability (Fig. A.3a), foraging suitability (Fig. A.3b) and likelihood of movement (Fig. A.3c) there is a similar pattern of change in the outputs samples. With a decrease of these variable, there was a decrease in potential pollination throughout the area (Fig. A.4a, b, c) and the variation in the sample was reduced. By increasing the value of these variables, the output values increased considerably in some regions, while others remain with a low final value (Fig. A.3a, b, c). Therefore, the variation in the potential pollination values of the area increased with each addition of a multiple of the standard deviation (Fig. A.4a, b, c).

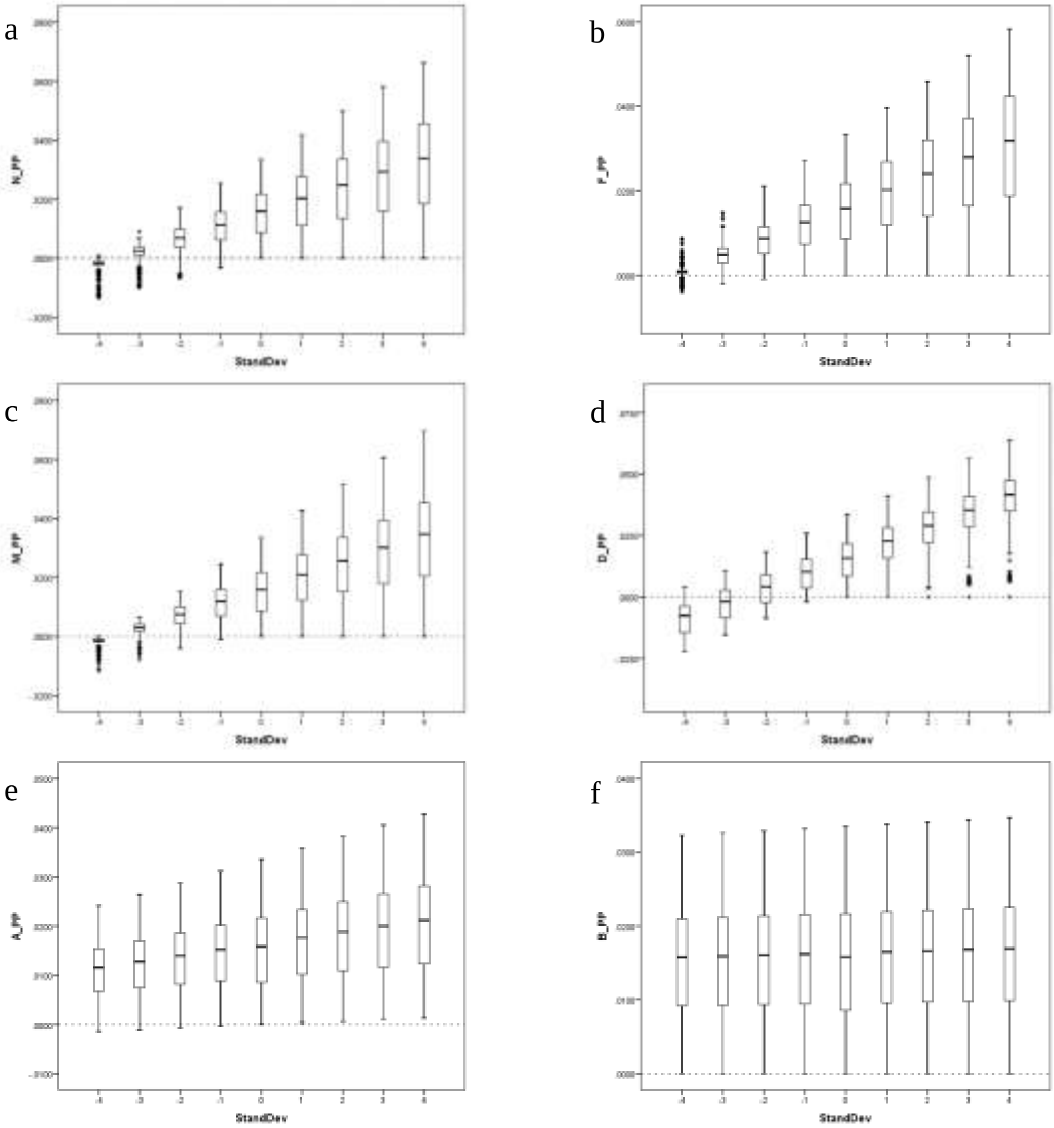
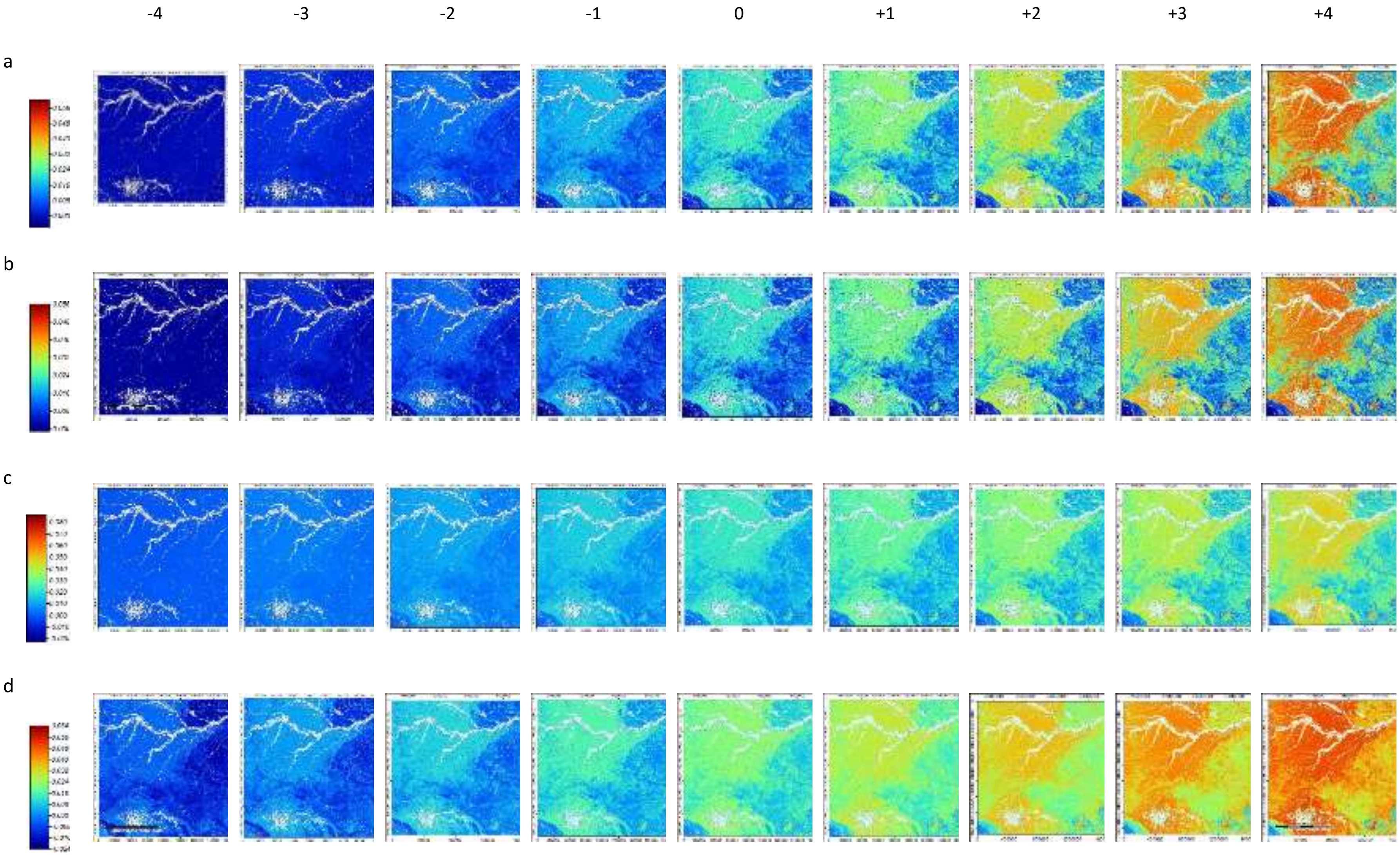


Figure A.3. Response of potential pollination (PP) model output when each input variable is modified by a factor of their respective standard deviation. The y-axis shows the potential pollination values obtained after the modification of each variable.a) nesting suitability, b) foraging suitability, c) likelihood of movement, d) foraging distance, e) foraging activity and e) density of barriers.


-4
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a
b
c
d

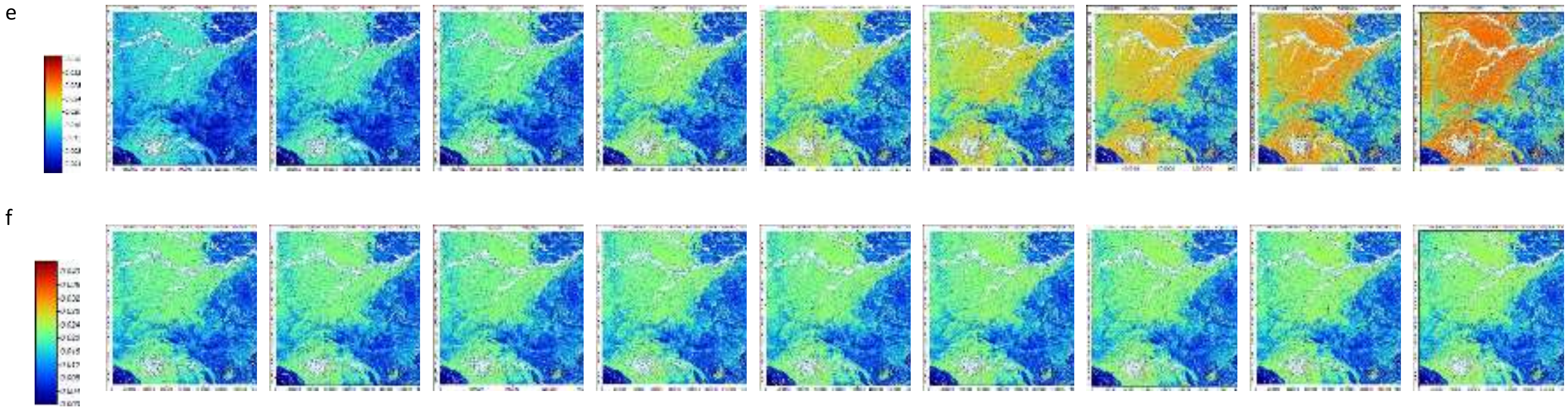


Figure A.4. Change of potential pollination model maps when each input variable is modified by a factor (±4) of their respective standard deviation, where 0 shows the original output map and a) nesting suitability, b) foraging suitability, c) likelihood of movement, d) foraging distance, e) foraging activity and e) density of barriers.

The variation in foraging distance values showed a mostly consistent increase or decrease in the output map values throughout the study area, depending on whether a multiple of the standard deviation was added or subtracted (Figs. A.3d, A.4d). Similarly, when foraging activity was modified there was a consistent variation of the output (Figs. A.3e, A.4e). However, the increase or decrease in the output map values was not as noticeable as the obtained with the modification of the foraging distance variable.

The modification of the input density of barriers showed the lower effect on the outputs, with a barely noticeable increase or decrease in the mean and variation of the samples (Fig. A.3f) and change in the output maps (Fig. A.4f).

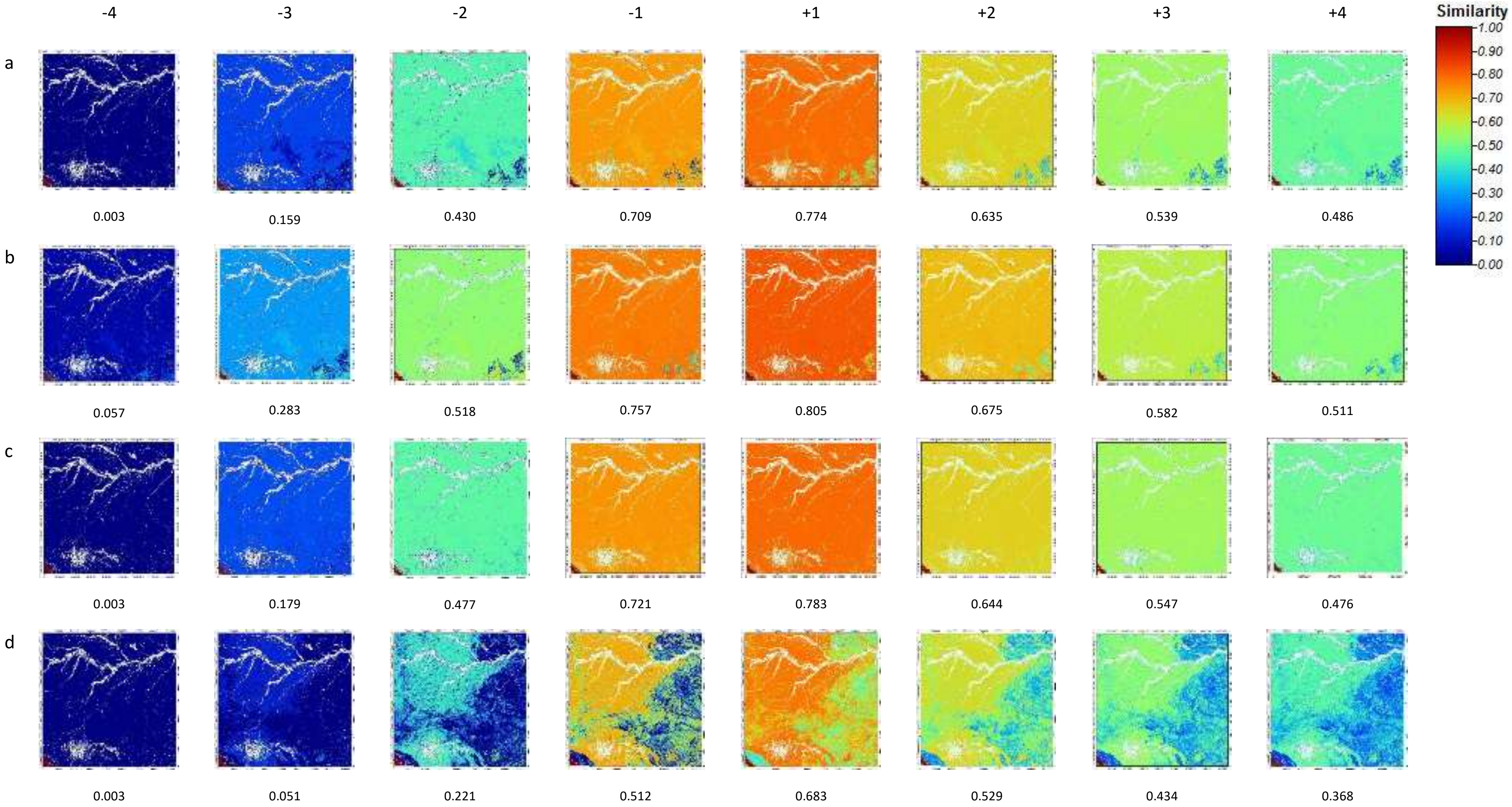
Given the results of the correlation analysis, where the slope for foraging was significantly correlated to all the continuous variables, and regression analysis, where the slope for nesting was identified as a non-informative variable for the model, the variables related to slope were excluded from the model and were not included in the one-at-a-time sensitivity analysis.

Figure 5 summarizes the comparison between the original output and each of the modified inputs, showing the degree of similarity per pixel. The variation of nesting suitability and foraging suitability changed pixel values throughout the area, mainly with the decrease of the values of the variables as a result of subtracting multiples of their respective standard deviation (Fig. A.5a, b). A significant change was observed in the southeast, an area dominated by rainfed croplands, which has a score of 0.2 for both nesting suitability and provision of floral resources.

When the likelihood of movement was modified there was a consistent change all over the area, except the in the pixels edging different land cover types, where the probability of movement decreases if the land cover type surrounding such pixels has a lower nesting suitability value. A different pattern of change resulted from the modification of foraging distance, where the main changes occurred eastwards. This area corresponds to the areas where the original variable had the lowest values.

The southwest region showed a consistent pattern of high similarity with the original output when all the inputs were modified, excepting foraging activity (Fig. A.5e). This region has the highest elevation and lowest temperature of the area; therefore, the foraging activity is lower than any other region. When the foraging activity was varied, it is here where the major changes occurred.

Finally, unlike the other inputs where the effects were evident throughout the area, the variation of the density of barriers affected only on those pixels where barriers are present (Fig. A.5f). These correspond to less than 1% of the total extent, hence the high similarity among the outputs.


-4
-3
-2
-1
+1
+2
+3
+4
Similarity
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
a
0.003
0.159
0.430
0.709
0.774
0.635
0.539
0.486
b
0.057
0.283
0.518
0.757
0.805
0.675
0.582
0.511
c
0.003
0.179
0.477
0.721
0.783
0.644
0.547
0.476
d
0.003
0.051
0.221
0.512
0.683
0.529
0.434
0.368

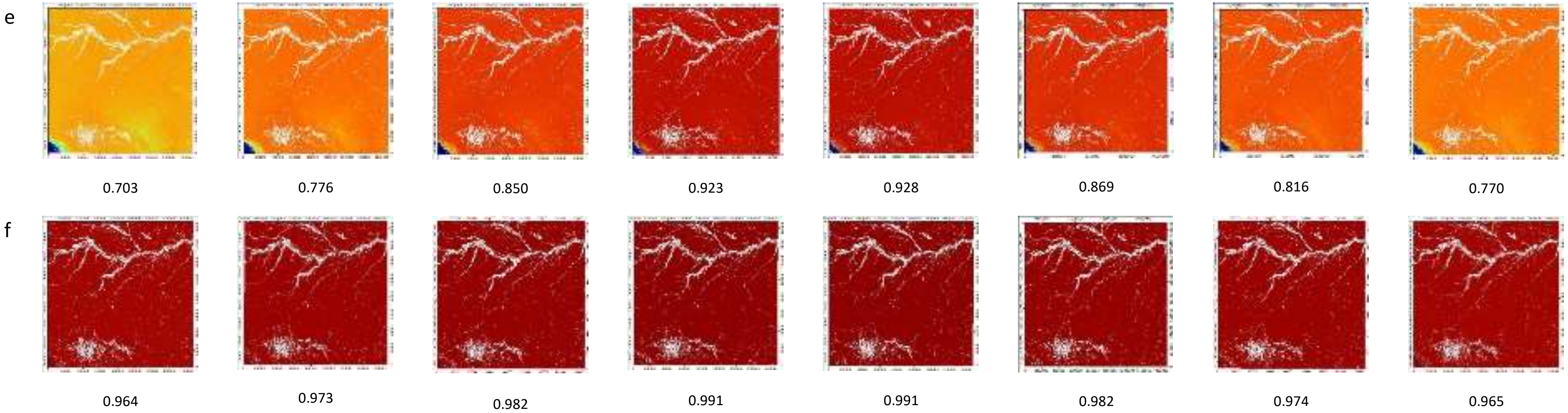


Figure A.5. Similarity between the original output of the potential pollination model and the output after the variation of the inputs (±4 standard deviation), where 1 is a complete similarity between the pixels and 0 complete difference. The number below each map denotes the overall similarity between the maps estimated using the Fuzzy numerical statistic s (Visser and Nijs, 2006). This statistic calculates the overall similarity as $s\ (a, b) = 1 - \frac{|a-b|}{\max\ (|a|,|b|)}$, where a is the original map and b is the map produced after the modification of a variable. a) nesting suitability, b) foraging suitability, c) likelihood of movement, d) foraging distance, e) foraging activity f) density of barriers.

Discussion and conclusion

These set of sensitivity analyses allowed to simplify the model by identifying redundant and non-informative variables, to assess the contribution of the variables to the output, and to identify interaction among variables with the backward selection method. First, redundancy of the inputs was discarded for the variables treated as continuous variables.

After analysing the effect of different correlation thresholds on the performance of different model types, Dormann et al. (2013) suggest a correlation coefficient > 0.7 as an appropriate indicator for when the correlation between variables affects model estimation and prediction. Although these variables showed some degree of correlation, it is likely to have no impact on the model performance given their correlation coefficients (<0.5).

The variables treated as categorical, slope for nesting and slope for foraging, were removed from the final model, given their effect on the other variables and the null or low relevance on the response. Although the evidence suggests that slope is an important factor for pollinator abundance (Taylor and Cameron, 2003; Makino, 2008), the spatial resolution at what this model was built (300 m) does not capture the variation per pixel relevant for pollinators, and it does not add information to the model at this scale, this may vary if the model resolution is downscaled.

Decreases in the inputs caused a reduction in the potential pollination per pixel throughout the area. However, increases in some of the inputs did not cause an increase for all pixels, showing that the interaction among the variables can lead to a reduced pollination potential. An increase in nesting or foraging suitability or a high probability of movement does not increase pollination unless activity and foraging distance are increased.

The high importance of foraging distance as an explanatory variable indicates that a change in the approach taken to estimate of pollinator’s foraging distance could significantly change the model output. This is supported by the high overall difference founded when the foraging distance input changed in the one-at-a-time variation analysis.

Regarding the input density of barriers, while the overall difference between maps was small due to the high frequency of pixels where barriers are absent, the regression analysis showed that by interacting with other inputs, it has a significant effect on the cells where these occur.

In general, the areas that showed the main change relative to the original output were those where the original input had the lowest values. In terms of the overall change between maps, the modification of foraging distance led to the highest change, followed by the likelihood of movement and foraging suitability.

Statistical analyses supplementary tables

a) Mann-Whitney U test using slope for nesting (Ns) and slope for foraging (Fs) as grouping variables to assess their effect on the remaining inputs.

		A	B	D	F	M	N
Ns	U	12591	64988	23982	53678	66230.5	40456
	Sig.	0	0.561175	0	0.170498	0.965503	0.005442
Fs	U	5062861	11058220	824602	10423779	10520897	9681980
	Sig.	0	0.006682	0	0	0	0

b) Linear regression analysis for the response variable potential pollination (PP)

Variables Entered/Removed [a]

Model	Variables Entered	Variables Removed	Method
1	Ns, M, N, B, A, Fs, F, D[b]		Enter
2		Ns	Backward (criterion: Probability of F-to-remove >= .100)

a. Dependent Variable: PP
b. All requested variables entered

Model Summary [c]

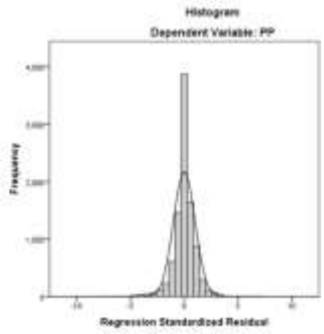
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.970[a]	0.941	0.941	0.0018928748
2	.970[b]	0.941	0.941	0.0018930350

a. Predictors: (Constant), Ns, M, N, B, A, Fs, F, D
b. Predictors: (Constant), M, N, B, A, Fs, F, D
c. Dependent Variable: PP

ANOVA [a]

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	0.543	8	0.068	18928.162	.000[b]
	Residual	0.034	9513	0.000		
	Total	0.577	9521			
2	Regression	0.543	7	0.078	21628.152	.000[c]
	Residual	0.034	9514	0.000		
	Total	0.577	9521			

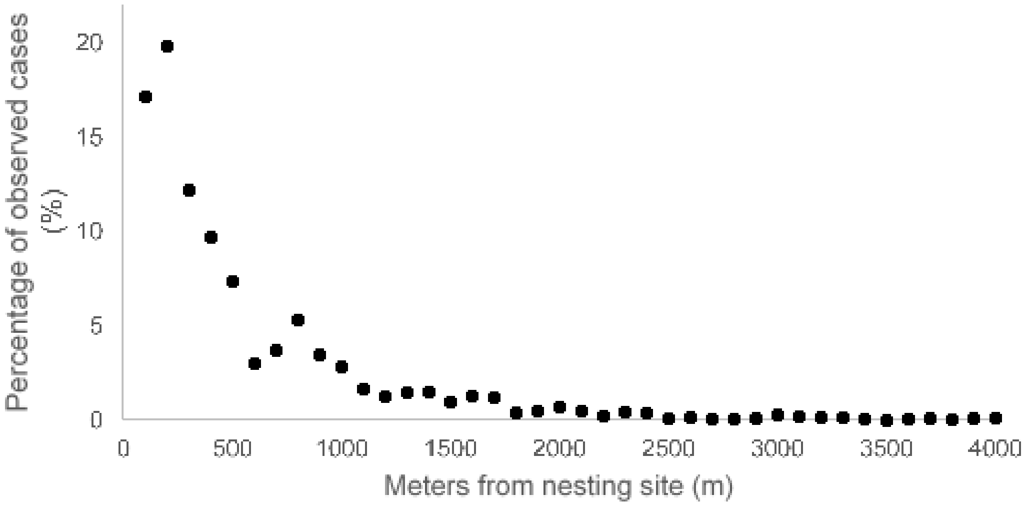
a. Dependent Variable: PP
b. Predictors: (Constant), Ns, M, N, B, A, Fs, F, D
c. Predictors: (Constant), M, N, B, A, Fs, F, D



Appendix B. Pantropical pollination

Figure B.1. Pollinators' foraging distance**.** a) Average proportion of cases observed every 100 meters from the nest for six tropical bee species, b) Weight applied to suitability scores to provide floral resources, calculated as a function of distance from nesting sites.

a



b

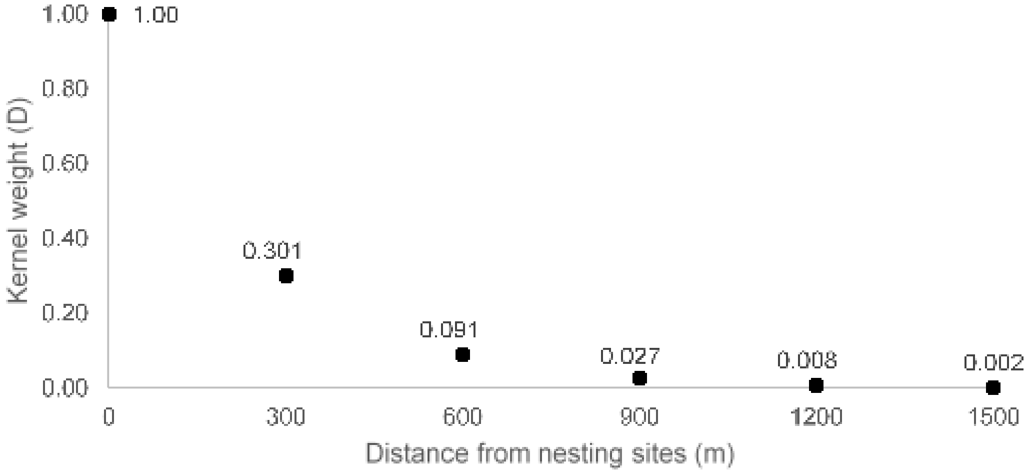


Table B.1. Bee species. Species used to calculate insect pollinator's foraging distance, size and reference.

Species	Body length (mm)	Reference
Apis florea	8 – 10	Abrol (1988)
Apis cercana	9 – 11	Dyer and Seeley (1991)
Apis melifera	11 – 13	Gary et al. (1972)
Apis dorsata	12 – 14	Dyer and Seeley (1991)
Xylocopa flavorufa	20 – 26	Pasquet et al. (2008)
Bombus terrestris	20 – 23	Walther-Hellwig and Frankl (2000)

Table.B.2. Daylight hours per year. The model of Forsythe et al. (1995) was used to calculate daylight hours per latitude degree

$D = daylength$
$L = latitude$
$J = day\ of\ the\ year$
$P = daylight\ coefficient$

$$P = asin\,(.39795 * cos(.2163108 + 2 * atan(.9671396 * tan(.00860(J - 186)))))$$

$$D = 24 - (24/pi) * acos\,((sin(0.8333 * pi/180) + sin(L * pi/180) * sin(P))/cos(L * pi/180) * cos(P))$$

Table B.3. Pollinator-dependent crops. The distribution of these dependent or highly-dependent tropical crops (Roubik, 1995; Klein et al., 2007) included in the 'Other crops' category of the 'Geographic distribution of major crops across the World' map (Leff et al., 2004) was used to model realised pollination

Subcategory	Crops
Nuts	Cashew nut
Oil-bearing crops	Coconut, melon seed
Vegetables	Pumpkin, cucumber, gherkin, watermelon
Fruits	Apple, pear, apricot, sour cherry, peach, plum, kiwi fruit, mango, avocado
Spices	Pimiento, vanilla, cinnamon, cardamom, fennel
Others	Coffee, cocoa

Appendix C. Projected pollination

Table C.1 Reclassification table. Nesting suitability (N_j) and floral resources (F_j) scores reclassified per pixel according to the projected percentage of forest loss. The pixels where no deforestation was projected maintained their original score.

ID	GlobCover land cover type	N_j				F_j			
		From	To			From	To		
			0.1-0.5	0.5-0.7	>0.7		0.1-0.5	0.5-0.7	>0.7
11	Post-flooding or irrigated croplands (or aquatic)	0.4	0.2	0.2	0.2	0.4	0.2	0.2	0.2
14	Rainfed croplands	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
20	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)	0.7	0.7	0.2	0.2	0.75	0.75	0.2	0.2
30	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	0.75	0.75	0.7	0.2	0.7	0.7	0.75	0.2
40	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)	0.8	0.75	0.7	0.2	0.9	0.7	0.75	0.2
50	Closed (>40%) broadleaved deciduous forest (>5m)	0.8	0.75	0.7	0.2	0.9	0.7	0.75	0.2
60	Open (15-40%) broadleaved deciduous forest/woodland (>5m)	0.4	0.2	0.2	0.2	0.45	0.2	0.2	0.2
70	Closed (>40%) needleleaved evergreen forest (>5m)	0.8	0.75	0.7	0.2	0.3	0.7	0.75	0.2
90	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)	0.4	0.2	0.2	0.2	0.15	0.2	0.2	0.2
100	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)	0.8	0.75	0.7	0.2	0.6	0.7	0.75	0.2
110	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	0.9	0.75	0.7	0.2	0.9	0.7	0.75	0.2
120	Mosaic grassland (50-70%) / forest or shrubland (20-50%)	0.9	0.75	0.7	0.2	0.9	0.7	0.75	0.2
130	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)	0.9	0.75	0.7	0.2	1	0.7	0.75	0.2
140	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	0.4	0.2	0.2	0.2	0.4	0.2	0.2	0.2
150	Sparse (<15%) vegetation	0.7	0.2	0.7	0.2	0.35	0.2	0.75	0.2
160	Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily)	0	0	0	0	0	0	0	0
170	Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water	0	0	0	0	0	0	0	0
180	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil	0	0	0	0	0	0	0	0
190	Artificial surfaces and associated areas (Urban areas >50%)	0.3	0.2	0.2	0.2	0.3	0.2	0.2	0.2
200	Bare areas	0	0	0	0	0	0	0	0
210	Water bodies	0	0	0	0	0	0	0	0
220	Permanent snow and ice	0	0	0	0	0	0	0	0
230	No data (burnt areas, clouds)	NoData	NoData	NoData	NoData	NoData	NoData	NoData	NoData

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