



Climate change impacts on the distribution of key tree species used by lion tamarins in the Brazilian Atlantic Forest: Applications to conservation

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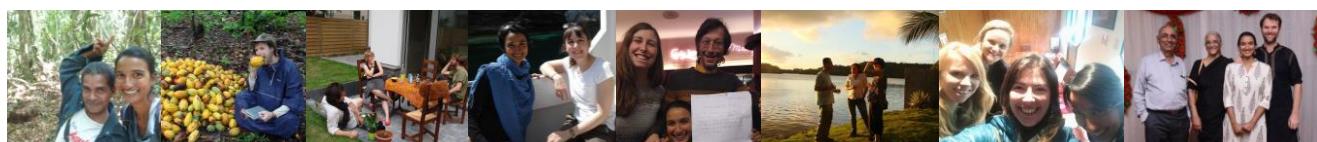
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Executive summary

To quote President Barack Obama, at the United Nations Climate Change Summit in 2014, “There is one issue that will define the contours of this century more dramatically than any other, and that is the urgent threat of a changing climate”. Mounting evidence has shown the impacts a changing climate has on species, flora and fauna – it can provoke changes in distributions, physiology, phenology, and behaviours, which in turn can lead to extinctions within the natural world, and a subsequent loss of ecological processes. The Brazilian Atlantic Forest (BAF), once stretching continuously from northern Brazil to northern Argentina is now heavily fragmented, and could be a portentous indicator for other ecosystems that also experience degradation. As the forest is converted, endemic fauna and flora lose their habitats, and various functions that maintained the ecosystems are also under threat. The small-bodied, endemic *Leontopithecus chrysomelas* can play a starring role in our understanding on what happens to regenerative processes in heavily defaunated and degraded forests. This thesis considers potential impacts of climate change on tree species distribution in the BAF, focused on seed dispersal and plant-animal interactions as a symptom of ecosystem functionality, and finally propose a method to incorporate seed dispersal into vegetation modelling, and use the outputs to consider how to implement various conservation and policy measures.

MaxENT (Maximum Entropy model – an ecological niche-based model) results for two future scenarios in four general circulation models suggest that up to 75% of the species risk losing more than half of their original distribution. CARAIB (CARbon Assimilation in Biosphere dynamic vegetation model) simulations are more optimistic in scenarios with and without accounting for potential plant-physiological effects of increased CO₂, with less than 10% of the species losing more than 50% of their range. Potential gains in distribution outside the original area do not necessarily diminish risks to species, as the potential new zones may not be easy to colonise. It will also depend on the tree species’ dispersal ability. This research highlights the importance of choosing the appropriate modelling approach and interpretation of results to understand key processes.

Our results from the field suggests that the dispersal behaviour and short daily-trajectories of *L. chrysomelas* (golden headed lion tamarins; GHLTs) may play a small role in regeneration of the forest because it is only a short-range disperser. Nevertheless, it probably contributes to increase the prevalence of its resource tree species locally, and thus likely to have a function in maintaining tree diversity by preventing local extinction.

In this field site, we were fortunate to have observed, sometimes only briefly, sloths, toucanets, tayras, kinkajous, hawks, various snake species (including one potentially mimicking the coral snake), and my field assistant (who had previously worked with *Sapajus xanthosternus* for 10+ years) confirmed that he heard vocalisations of the capuchins one morning. Additionally, the few evenings when the GHLTs were late arrivals to their sleeping sites, bats (unrecognisable to me at species level) were also seen flying around the trees. It was also always amusing to see beautifully intricate little frogs jumping up from puddles after rainy evenings. While defaunation and degradation are problems and must be confronted, it can be hopeful to know that even these areas can be home to the intrepid, beautiful, slithery, diversity that makes the BAF the hotspot it is.

The principal conclusion from both modelling and field work, is that conservation actions, both in the field, and at policy levels are mandatory for the conservation and functionality of the Brazilian Atlantic Forest.

Sumário executivo

Na Cúpula das Nações Unidas sobre Mudança Climática em 2014, o presidente Barack Obama expressou que, “Há um assunto que definirá os contornos deste século de forma mais dramática do que qualquer outra, e essa é a ameaça urgente de um clima em mudança”. As evidências sobre os impactos das mudanças climáticas nas espécies, tanto na flora e na fauna, estão crescendo – a mudança climática pode provocar alterações nas distribuições, fisiologia, fenologia e comportamentos que, por sua vez, pode levar a extinções e uma subsequente perda de processos ecológicos. A Mata Atlântica brasileira (BAF em inglês), que no passado tinha uma distribuição contínua do norte do Brasil até o norte da Argentina, está agora fortemente fragmentada e pode ser um indicador importante para outros ecossistemas que também sofrem degradação. À medida que a floresta é convertida, a fauna e flora endêmicas perdem seus habitats, e várias funções que mantêm os ecossistemas também estão ameaçadas. O *Leontopithecus chrysomelas*, um macaco de pequeno porte endêmico do Brasil, poderia desempenhar um papel nos processos regenerativos em florestas altamente defaunadas e degradadas. Esta tese considera potenciais impactos da mudança climática na distribuição de espécies arbóreas do BAF, focada na dispersão de sementes e interações planta-animal como um sintoma da funcionalidade do ecossistema, e finalmente propõe um método para incorporar a dispersão de sementes na modelagem dinâmico de vegetação e usar os resultados para considerar como implementar várias medidas de conservação e influenciar a política ambiental.

Os resultados de MaxENT (modelo de entropia máxima - um modelo de nicho ecológico) para dois cenários futuros em quatro modelos de circulação geral sugere que até 75% das espécies estão sob risco de perder mais da metade de sua distribuição original. As simulações de CARAIB (assimilação de carbono na biosfera, um modelo dinâmico da vegetação) são mais otimistas em cenários, com e sem explicação dos potenciais efeitos fitossanitários do aumento de CO₂, com menos de 10% das espécies perdendo mais de 50% da sua distribuição. Potenciais ganhos na distribuição fora da área original não diminuem necessariamente os riscos para as espécies, dado que as novas zonas potenciais podem não ser fáceis de colonizar. Dependerá também da capacidade de dispersão das espécies de árvores. Esta pesquisa destaca a importância de escolher a modelagem apropriada e a interpretação dos resultados para entender os principais processos ecológicos.

Nossos resultados sugerem que o comportamento de dispersão e as curtas trajetórias diárias de *L. chrysomelas* (mico leão de cara dourada; GHLT em inglês) podem ter um papel limitado na regeneração da floresta, porque é apenas um dispersor de curto alcance. No entanto, provavelmente contribui para aumentar a prevalência de algumas espécies de árvores preferenciais localmente e, portanto, provavelmente terá uma função na manutenção da diversidade de árvores, evitando a extinção local.

Na área de estudo observamos preguiças, tucanos, irara, jupará, falcões, várias espécies de cobras (incluindo uma potencialmente imitando a cobra coral), e meu assistente de campo (que já havia trabalhado com *Sapajus xanthosternus* por mais de 10 anos) confirmou que ele ouviu vocalizações dos capuchinhos uma manhã. Além disso, nas poucas noites em que os micos chegavam tarde a seus ocos, os morcegos (que não reconheço ao nível das espécies) também eram vistos, voando ao redor das árvores. Era sempre divertido ver pequenas rãs intrincadas e delicadas pulando de poças após as noites chuvosas. Embora a defaunação e a degradação sejam problemas e devam ser enfrentados sem demora, dá esperança que essas mesmas áreas possam abrigar ainda uma diversidade fascinante, bela, e escorregadia que faz do BAF um "hotspot".

A principal conclusão da modelagem e do trabalho de campo é que as ações de conservação, tanto no campo quanto nos níveis de políticas, são obrigatórias para a conservação e a funcionalidade da Mata Atlântica brasileira.

Résumé

Lors du sommet des Nations Unies sur le changement climatique en 2014, le président Barack Obama a exprimé son inquiétude : « il y a un problème qui définira le déroulement de ce siècle plus dramatiquement que tout autre, et c'est la menace pressante du changement climatique ». L'évidence croissante de l'impact du changement climatique sur la faune et la flore a montré que celui-ci peut provoquer des changements dans la répartition, la physiologie, la phénologie et les comportements, pouvant conduire à des extinctions dans le monde naturel et à une perte ultérieure de processus écologiques. La forêt atlantique brésilienne (BAF en anglais), qui s'étendait jadis de manière continue du nord du Brésil au nord de l'Argentine, est maintenant très fragmentée et pourrait constituer un indicateur de mauvais augure pour d'autres écosystèmes également dégradés. Au fur et à mesure que la forêt est convertie, la faune et la flore perdent leurs habitats, et, diverses fonctions qui ont maintenu les écosystèmes sont également menacées. *Leontopithecus chrysomelas*, une espèce de singe endémique et de petite taille, pourrait jouer un rôle dans l'évolution des processus de régénération dans les forêts fortement défaunées et dégradées. Cette thèse examine les impacts potentiels du changement climatique sur la distribution des espèces d'arbres dans le BAF, en se concentrant sur la dispersion des graines et les interactions plantes-animaux en tant que symptôme de la fonctionnalité de l'écosystème, et propose enfin une méthode pour incorporer la dispersion des graines dans la modélisation de la végétation et examiner comment mettre en œuvre diverses mesures de conservation et politiques environnementales.

Les résultats de MaxENT (modèle d'entropie maximale - un modèle basé sur une niche écologique) pour deux scénarios futurs dans quatre modèles de circulation générale suggèrent que jusqu'à 75% des espèces risquent de perdre plus de la moitié de leur répartition d'origine. Les simulations de CARAIB (modèle dynamique d'assimilation du carbone dans la biosphère) effectuées aussi bien avec que sans les effets physiologiques potentiels de l'augmentation de CO₂ sur les plantes, sont plus optimistes dans les scénarios, avec moins de 10% des espèces perdant plus de 50% de leur aire de répartition. Les gains potentiels de distribution en dehors de la zone d'origine ne réduisent pas nécessairement les risques pour les espèces, car les nouvelles zones potentielles peuvent ne pas être faciles à coloniser. Cela dépendra également de la capacité de dispersion de l'espèce. Cette recherche souligne l'importance de choisir l'approche de modélisation et l'interprétation des résultats appropriées pour comprendre les processus clés.

Nos résultats sur le terrain suggèrent que le comportement de dispersion et les courtes trajectoires quotidiennes de *L. chrysomelas* (tamarin lion à tête dorée ; GHLT en anglais) pourraient jouer un rôle peu important dans la régénération de la forêt car il ne s'agit que d'une dispersion à courte distance. Néanmoins, il contribue probablement à augmenter la prévalence de ses espèces d'arbres préférées localement, et donc probablement jouerait un rôle dans le maintien de la diversité des arbres en empêchant leur extinction locale.

Sur ce site, nous avons eu la chance d'avoir observé, parfois brièvement, des paresseux, des toucanets, des tayras, des kinkajous, des faucons, diverses espèces de serpents (dont une imitant potentiellement le serpent corallien) et mon assistant de terrain (qui avait déjà travaillé avec *Sapajus xanthosternus* pendant plus de 10 ans) a confirmé avoir entendu des vocalisations de capucins un matin. De plus, les quelques soirées où les GHLTs arrivèrent tardivement sur leurs sites dortoirs, des chauves-souris (dont l'espèce m'est inconnue) ont également été observées volant autour des arbres. Il était également toujours amusant de voir des petites grenouilles admirablement complexes sauter des flaques après des soirées pluvieuses. Bien que la défaunation et la dégradation soient des problèmes urgents à confronter sans délai, on peut espérer quand même que ces zones puissent abriter la diversité belle et subtile qui fait de la BAF le « hotspot » qu'elle est.

La conclusion principale de la modélisation et des travaux sur le terrain est que les mesures de conservation, tant sur le terrain que sur le plan politique, sont obligatoires pour la conservation et la fonctionnalité de la forêt atlantique brésilienne.

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1 Introduction

Why study climate change

(AKA – why did I do this research again?)

To quote President Barack Obama, at the United Nations Climate Change Summit in 2014, “There is one issue that will define the contours of this century more dramatically than any other, and that is the urgent threat of a changing climate”. Fortunately, this thesis will not discuss the politics behind addressing climate risks. Instead, the research outlines some of the tools and methods to understand potential impacts of climate change on organisms in the Brazilian Atlantic Forest.

Answering the question, “Why study climate change?” is an easy one. Mounting evidence has shown the impacts a changing climate has on species, flora and fauna – it can provoke changes in distributions, physiology, phenology, and behaviours, which in turn can lead to extinctions within the natural world, and a subsequent loss of ecological processes.

Considering the facility in answering “why”, we can already step into murkier questions such as, “How will species and ecosystems react under the future climates?”. There are no obvious answers. First, uncertainties arrive with future climate predictions. Not only are there large differences between climate model outputs, but they also depend on the socio-economic conditions which will prevail in the next decades. There are fewer doubts regarding the range of temperature increase, but confidence on precipitation changes remains low (Paeth et al. 2013). Second, the focus on the many phenomena affected by climate change in the living world reveals incomplete knowledge or even understanding of processes and interactions and affects our ability to make robust predictions for the future. The phenomena include migratory processes, i.e. seeking climatically appropriate zone; the interactions between the species, for example, pollination and budding; acclimation, the processes by which the organisms adjust their metabolism and morphology more or less rapidly to prevalent conditions, among others. An example is provided by (Reich et al. 2016). In their study, respiration only increased by 5% in native juvenile trees grown under a 3.4 °C temperature warming while the increase would reach 23% in non-acclimated plants, thus an 80% difference; but the estimated acclimation was much stronger than the effects observed in two other recent works (only 30% difference; idem). Another important aspect is that the world is changing independently of climate change, including pollution, land-use changes, technology, population growth and/or poverty progression (Malhi et al. 2014). Nevertheless, despite the difficulties, by studying the potential impacts of climate change on the natural world, by setting milestones of possible futures for species and ecosystems, we can help

conservation practitioners and other relevant stakeholder assess risks and vulnerability, and, when possible, take appropriate actions.

This leads us to a more challenging question on “How to study climate change impacts”. There are very large bodies of organized scientific knowledge that can be used to study the effect of climate change. The information on organism distribution and their traits has increased substantially thanks to collations of georeferenced data from herbaria, museums, research projects, etc. such as the Global Biodiversity Information Facility (James et al. 2018), Tropicos, the botanical information system at the Missouri Botanical Garden, RAINBIO covering sub-Saharan tropical Africa (Dauby et al. 2016) or TRY for plant traits (Kattge et al. 2011). These data allow us to model the climate conditions the organisms prefer, which could later be used to infer the future. In situ, large scale experiments are conducted on the effects of elevated temperatures, increase air CO₂ concentration, reduced precipitations, etc. on organisms to understand their responses in the new conditions (e.g. Agathokleous et al. 2016; Duursma et al. 2016; Sánchez-Carrillo et al. 2018; Purcell et al. 2018). Ecosystem analysis studies explain, with growing precision, the consequences of human disturbances in particular, like forest loss and excessive hunting (e.g. Pessoa et al. 2016; Rocha-Santos et al. 2017; Trolliet et al. 2017) which are other key factors of major changes in tropical ecosystems and influencing the distribution and interactions of organisms. Finally, remote sensing analyses map the evolution of the ecosystem distribution and properties and allow understanding the dynamics of fragmentation (Mitchard et al. 2011; Taubert et al. 2018; Song et al. 2018).

Through this research, we present our method of choice to study the effects of climate change on organisms and ecosystems, which is mechanistic modelling. Such a methodology provides a platform to integrate processes and quantify the complex interactions occurring in ecosystems as well as in mosaic systems made of forest patches, crops, or intermediate habitats (Fontaine et al. 2014). These are the reasons why we used and tested these tools.

Choosing the study species and region was relatively easy. Besides a personal fondness for the frugivore in question, *Leontopithecus chrysomelas* (at under 600 grams as adults, with an eye-catching orangey-black mane, they are easy to admire), there was also the dire interest in learning about degraded ecosystems. Unfortunately, the need to understand functional losses in degraded ecosystems has become more relevant to design effective conservation strategies. The Brazilian Atlantic Forest (BAF), once stretching continuously from northern Brazil to northern Argentina is now heavily fragmented and could be a portentous indicator for other ecosystems that also experience degradation. As the forest is converted, endemic fauna and flora lose their habitats, and various functions that maintained the ecosystems are also under threat. The small-bodied, endemic *L. chrysomelas* can play a starring role in our understanding on what happens to regenerative processes in heavily defaunated and

degraded forests. This thesis considers potential impacts of climate change on tree species distribution in the BAF, focusing on seed dispersal and plant-animal interactions as a symptom of ecosystem functionality, and finally proposes a method to incorporate seed dispersal into vegetation modelling, and use the outputs to consider how to implement various conservation and policy measures.

In summary, the research on “**Climate change impacts on the distribution of key tree species used by lion tamarins in the Brazilian Atlantic Forest: Applications to conservation**” will

- discuss key modelling methods available to determine the links between climate and distributions of several tree species in future climate scenarios (Chapter 3);
- establish the potential role of an endemic primate species from the Brazilian Atlantic Forest (BAF) in the migration or conservation of tree species towards appropriate climates (Chapter 4);
- propose methods to couple dispersal with dynamic vegetation modelling and recommend conservation strategies to decrease vulnerability of at-risk tree species in the BAF, and protect the habitats of several BAF species (Chapter 5).

In Chapter 3, we present the differences in the potential distributions of 94 tree species from the BAF, which constitute the resources of *L. chrysomelas*, using two different modelling methods. Each model has trade-offs in terms of data requirements, time, and resolution, and the choice of model can be evaluated based on those criteria. A key conclusion from the different models is that neither a statistical nor a mechanistic model can account for critical ecosystem processes. Coupling a dynamic vegetation model with dispersal events may provide a more complete picture for future distributions, as climate is not the only factor that affects species’ presence.

Accounting for the principal observation, our study integrates field research (Chapter 4), where observed behaviours relating to foraging and dispersal were translated into a deterministic model of seed dispersal (MOST). The field work had two principal objectives, one to understand the extent to which GHTLs might play a role in seed dispersal, when confronted with seeds of the largest size they are able to swallow, and secondly to understand how to parameterise their behaviours to be replicated into a movement and dispersal model.

Chapter 5 discusses the coupling of MOST with CARAIB. Time-constraints precluded the actual coupling, though the chapter outlines how even data from literature could be used to adapt MOST and using the net-primary productivity output from CARAIB as a proxy for growth, we can, in the future, simulate how long it could take for natural regeneration processes to occur in a fragmented landscape. Unsurprisingly, when accounting for other anthropic pressures, we recognise the

importance of conservation strategies, and policy adaptations that could help restore and protect one of the world's biodiversity hotspots.

The Brazilian Atlantic Forest

(AKA – places to visit before it's too late)

The original extent of the Atlantic Forest stretches from Rio Grande do Norte in Brazil, to northern Argentina, and Paraguay, with more than 90% of the biome present in Brazil. This biome is a biodiversity hotspot (Myers et al. 2000), with several endemic plant and animal species.

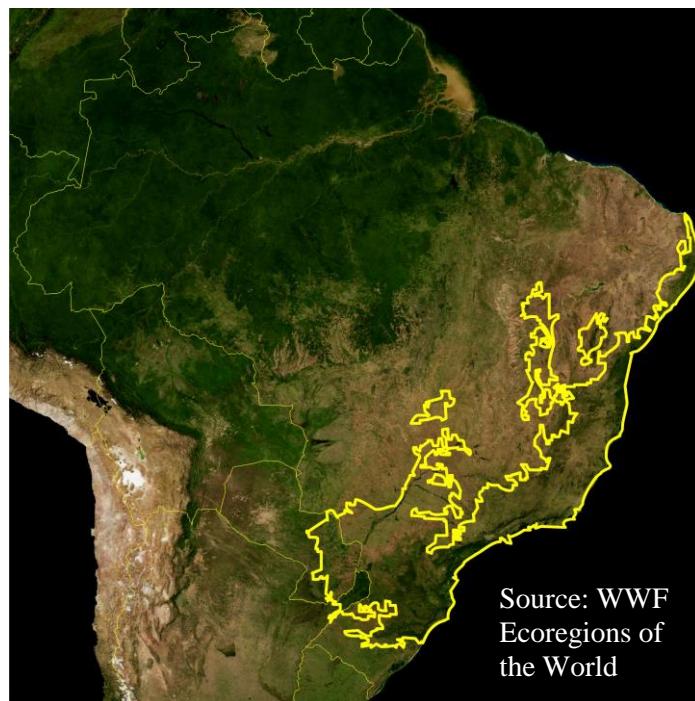


Figure 1.1 Original distribution of Atlantic Forest, including extent in Argentina and Paraguay.

The forests within the biome were classified into five types. Indeed, Oliveira-Filho and Fontes (2000), have demonstrated an influence of altitude and precipitation on the floristic composition. Joly et al. (2014) also made a case for describing the Atlantic Forest composition (dense ombrophilous, open ombrophilous, mixed ombrophilous, semideciduous seasonal and deciduous seasonal) in a detailed manner, in addition to describing various ecosystem services that the biome provides, linked to this high level of diversity.

The key threats to the Atlantic Forest are habitat loss due to conversion for agriculture, logging (both illegal and unsustainable), and urbanisation. The Brazilian Atlantic Forest (BAF) houses approximately 100 million human residents, and contributes to 70% of the Brazilian gross domestic

product (Martinelli and Moraes 2013; Scarano and Ceotto 2015). These factors have led to a high level of fragmentation, up to 92%, increasing the biome's vulnerability and functionality as a hotspot.

Habitat loss and hunting have led to decreased population of the BAF fauna. With such high levels of fragmentation, BAF vegetation may be at additional risk from climate change, particularly if unable to colonise climatically favourable zones in the future (Zwiener et al. 2017). In the tropics, vegetation depends on frugivorous fauna, as much as the animals rely on plants. 80-90% of animal biomass corresponds to frugivores (Fleming et al. 1987; Estrada et al. 1993), while climax forests host a majority of zoothorax tree species (Peres and Roosmalen 2002). The BAF is no exception – many of the BAF tree species are zoothorax and rely on frugivorous fauna for its dispersal. At regional scale, tree species diversity seems preserved despite loss of abundances. It is likely that degraded habitats remain suitable habitats for many forest species, but mainly tree longevity may conceal time-lagged responses (Joly et al. 2014). When defaunation is coupled with fragmentation (Bogoni et al. 2018), the likelihood of vegetation being able to colonise new habitats is low. This poses a separate threat to the fauna in the BAF, that depend on the vegetation for their survival – as their habitat degrades with increasingly at-risk vegetation, their own risk increases.

Focal species (flora and fauna)

(AKA – cute and easy to spot: how to choose a study site)

Leontopithecus chrysomelas or Golden-Headed Lion Tamarins (GHLTs) are small bodied, arboreal primates occurring only in Southern Bahia and a small part of northern Minas Gerais, at the northern end of the BAF (Raboy and Dietz 2004). The eastern part of the GHLT range lacks seasonal precipitation and consists of evergreen forests. However, moving westwards, towards the drier *caatinga* area, the vegetation is semi-deciduous, largely due to the seasonality in precipitation (Rylands et al. 1991). They are frugivores, though a large part of their foraging activities is in search of insects and small vertebrates, particularly within liana conglomerates or bromeliads. They also consume gum, flowers, and young leaves in a much lower proportion compared to fruits. They live in multi-male, multi-female groups from 4 to 12 individuals, and both sexes of sub-adults are known to emigrate. They are territorial and engage in aggressive “encounter” behaviours, however, it is not uncommon to see more than one group sometimes foraging in the same area at a given time. GHLTs could be considered generalists, as they are able to survive in secondary forest habitat (Rylands 1996), as well as cacao agro-forestry systems, known as *cabrucá*. Indeed, this latter ability is critical for their survival, as more than 60% of the GHLT distribution is under *cabrucá* systems. However, not all *cabrucá* systems are managed to ensure the viability of GHLT presence (Oliveira et al. 2010). In various studies focusing on GHLT feeding ecology, the species has been observed consuming fruits, from up to 92 distinct species of trees, as well as flowers of several bromeliad species (Catenacci

2008). They do swallow and defecate seeds of some species, but their role as dispersers seems to depend on their habitat.



Figure 1.2 Photo of *L. chrysomelas* taken in Bahia © Denruyter

With such range-restricted endemic fauna, climate change impacts can be two-fold – first on the organism itself, though the principal reason for its endemism may not be due to the climate but rather habitat characteristics as suggested for *Sapajus nigritus*, another small primate endemic of the Brazilian Atlantic forest (Hedges et al. 2017); second, due to impacts on it habitat.

We can reasonably hypothesise that threats such as climate change, that can decrease habitat quality, will also impact species like tamarins. In the degraded biome, several forest fragments suffer from local defaunation, i.e. loss of larger-bodied fauna, leading to the “empty forest” scenario, which can lead to loss of important services such as seed dispersal, pollination, seed predation (Da Silva and Tabarelli 2000; Chiarello 2008), which maintain forest dynamics and on occasion, could be important for regeneration or connectivity. This means that zoochoric vegetation can rely only on small or medium bodied frugivores that may remain, increasing the risks for tree species with larger seed sizes. In such a context, the role of GHLTs may prove to be important in the maintenance of habitats, or to a limited extent, regeneration, though functionally, they may not be able to fulfil the entire range of services lost.

The choice for studying the dispersal of seeds from the *Pourouma* genus was principally linked to the seed size, besides other practical considerations related to duration of fruiting season. *Pourouma* seeds measure approximately 1.1 cm in length and 0.9 cm in width – any fruits consumed by the GHLTs with larger seed sizes will have the seeds immediately discarded via spitting, most commonly under the parent tree.

The *Pourouma* genus is a Neotropical one, and a recent review indicates 43 species. The genus is restricted to the Neotropics, with most diversity in the Amazon region, relative to the BAF. The trees are dioecious, with stilt-roots and, entire to palmatilobed leaves. Most *Pourouma* species are associated with “terra firme” (non-inundated) secondary forest at elevations up to 1000 m. According to (Neto and Gaglioti 2017), some species, particularly *P. guianensis*, are most often found in degraded areas, while other rarer species (*P. ellipitca*) are present in more undisturbed patches. In the GHLT range, the three most common species of *Pourouma* includes *P. mollis*, *P. velutina*, *P. guianensis*, and the monkeys have been observed eating fruits and swallowing seeds of all three species. The species tend to fruit synchronously, typically between October and April, and in some years, there has been a much shorter fruit availability in July as well. The mature fruits are a deep purple, quite pulpy, with sweet and sour tannin notes, particularly in the skin which can feel quite astringent. One added advantage of choosing this tree genus is that their saplings and seedlings are extremely easy to identify, facilitating germination studies as well as counts of adults, saplings, and seedlings within parcels.



Figure 1.3 Photos of *Pourouma* mature fruit (left), palmatilobed leaf (middle), and stilt roots (right). © Raghunathan

Additionally, by studying the uptake and possible influences that seed swallowing and defecation may have on the germination rates and survival for the largest seed size that the GHLTs can swallow, we can make *some* inferences on whether or not areas with high hunting pressure for large bodied frugivores suffer from loss of functional diversity and the possible role of GHLTs in regeneration. This was not the principal question of the research however!

Some challenges in studying climate impacts

(AKA – research is hard and here’s why)

Capturing how a changing climate might impact species, irrespective of the taxon, is difficult. Scientists and conservation practitioners typically rely on modelling, and each model has its own constraints.

Peterson et al. (2015) describes in some detail the main modelling methods, including their advantages and drawbacks. There are ecological niche-based models (ENMs), or species distribution models (SDMs) which use a correlational approach with varying degrees of statistical complexity (Elith and Leathwick 2009). Another modelling approach is mechanistic, based on biophysics and physiology, where the tolerances of a species under different environmental conditions are computed (e.g. Barve et al. 2014). Mechanistic or process-based modelling also measures responses of species based on their tolerances, but are also more complex as they can also include interactions (competition), dispersal/colonisation, etc. These kinds of process-based models of vegetation are also called dynamic vegetation models (DVMs; Dury et al. (2011); Snell et al. (2014)). Mechanistic and process-based modelling is less developed for animals, with fewer studies demonstrating this approach (Boyles et al. 2011). Few studies on climate impacts on animals have incorporated the physiological responses (Kearney and Porter 2009), possibly because the physiology of mammals and their competition may be harder to simulate. Additionally, process-based modelling (plant or animal) is definitely more time consuming, particularly with respect to the level of data required on the morphophysiological traits of the species' in question and with computing itself.

Bearing in mind the varying approaches, coupled with the differences in the climate data sets developed for several economic scenarios, there can be high levels of uncertainty in estimating climate change impacts. As such, conservation practitioners and decision-makers could benefit from identifying a range of possible climate impacts on their species of interest. Any consistent declining trends predicted by several models, in a number of scenarios, with multiple climate datasets will imply a higher risk of extinction due to climate change for those species.

Modelling the GHLT's physiological response to a changing climate would be very challenging, though as explained in Korstjens and Hillyer (2016) (chapter 11), small bodied mammals typically have higher metabolic rates, which are likely to increase with higher temperatures, and a corresponding larger energy expenditure. This could increase their vulnerability to climate change. However, a correlational approach may be impractical due to its endemic status, as we cannot know that climate reasons explain the endemism. Therefore, to understand the possible climate threats for this endangered species, we chose to simulate the potential impacts of climate change on the distribution of 94 tree species used by the GHLTs as food or sleeping site resources and evaluate the risks to the BAF habitat. Additionally, we studied the seed dispersal behaviour of the GHLTs in a mosaic habitat to understand the monkey's potential role in the colonization process of the vegetation.

The problem of seed dispersal

(AKA – collecting faeces is the easy part)

In tropical regions, the premise that habitats must be protected and resilient to climate change, particularly for its fauna, is directly affected by seed dispersal. Zochoric seed dispersal, which is a process that tropical vegetation relies on, is a process where animals consume fruit, and either swallow seeds that are defecated at a different time, and sometimes location, or store seeds in cheek pockets and are spat at a different location and time. In a first application of the dynamic vegetation model to some BAF tree species, we had identified that plant-animal interactions are too important to ignore, and as yet, are not adequately captured in vegetation modelling, mechanistic or otherwise (Raghunathan et al. 2015). Brooker et al. (2007) even argue that by not including dispersal interaction in climate modelling, there is a risk of not accurately understanding the pathways to collapse, particularly citing lower rates of long-distance dispersal that could drive extinction processes in mutualistic species. While seed dispersal is, in and of itself, an extremely complex process, in some instances it can be studied in a simplified model (as in this case, with one frugivore and one genus of fruit tree) and still be relevant for further research.

Difficulties in modelling seed dispersal is mostly linked to insufficient data on animal movements, gut-passage times, and other variables that are useful in predicting animal movement patterns, and germination success. However, the effort required to collect some additional data while conducting field work is only marginally more, while the added value of the data itself is quite high.

Combining MOST with a DVM. What could it produce?

(AKA – future research projects for incoming graduates)

The exercise in joining a dispersal module with a DVM is precisely to overcome the limitations of modelling plant growth only. Such a coupling could perhaps lend itself to scenario building, by creating landscapes of fragments and measuring dispersal rates of key species towards appropriate climates. Even if we were excluding an analysis based on climate change, CARAIB models have reasonably reproduced present-day distributions of various species, and such an exercise would be relevant to understand where to place corridors or stepping stones between patches, and even identify the appropriate species from an “attractor” perspective, but also from a productivity perspective. Such detailed tests were beyond the scope of this particular research and is therefore included here as an open invitation for further investigation. After all, they say a thesis is only as good as the number of new questions it produces.

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2 Research approach

First, start by putting together an effective team... Doctoral work is best accomplished as a joint endeavour.

The research question had two main methodological components: Modelling & Field work. While the field work does not entirely offset the outcome of bad seated postures, high screen time, and a sense of complete inadequacy (when confronting one's absolute lack of skills in programming), it is very useful to improve the model and helps the memory. Precisely when you continually ask the question, "What am I doing this for" the fieldwork will help you remember – it's for conservation, and we need all hands on-deck. This section provides an overview of the research methods.

CARAIB: CARbon Assimilation in the Biosphere

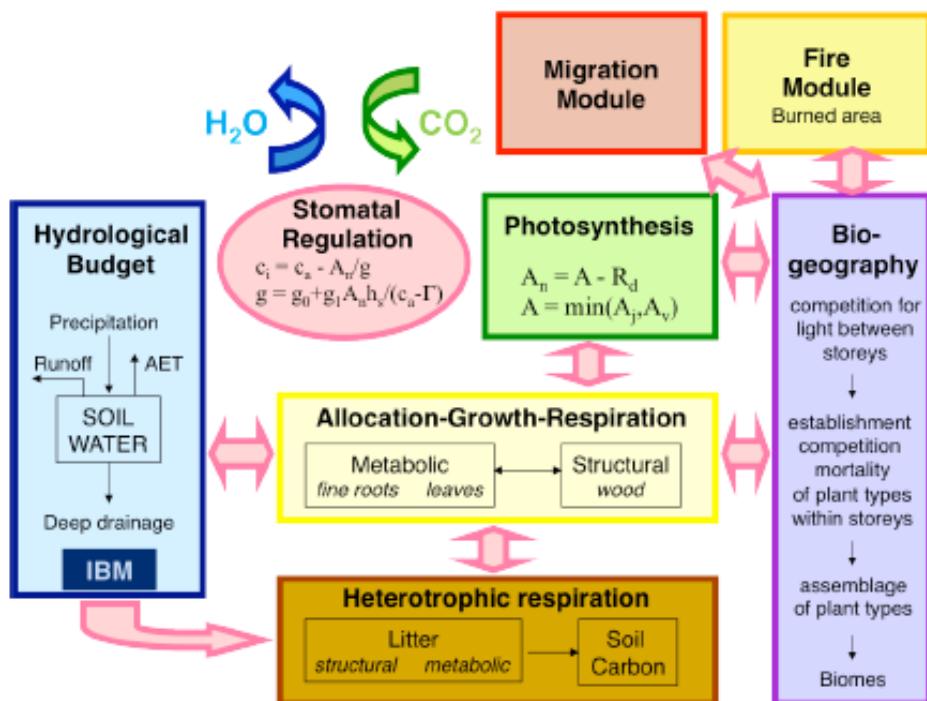


Figure 2.1 Diagrammatic representation of the CARAIB dynamic vegetation model (DVM).

The diagram is a schematic representation of the CARAIB dynamic vegetation model (DVM), which was first created in the early 90s by researchers in the Laboratory for Planetary and Atmospheric Physics, at the University of Liege, Belgium. CARAIB can simulate plant growth using a dynamic and mechanistic method that calculates key processes and interactions in the biosphere (terrestrial realm). Dury (2015) provides an excellent summary of the CARAIB modules and the specific calculations behind each. Previous models of CARAIB have been improved to highlight the

transient responses of ecosystems to future climates, rather than focusing only on carbon flows. This is reflected in updates in the modules' interactions, when simulating establishment, competition, and mortality of the plants of interest.

Each module captures specific interactions and dynamics, that are linked to other modules, and can affect the outcome of plant growth. For example, the hydrological budget component models the water cycle, considering aspects of precipitation, evapotranspiration, soil water levels (stored or run-off). When water levels are low, CARAIB simulates a “hydric stress” that influences stomatal conductance, which in turn affects photosynthesis, itself taking into account atmospheric CO₂ concentration, light and temperature. Soil water is influenced by soil texture, which is an input in the CARAIB model. These dynamics have a direct impact on plant respiration and photosynthesis balance and finally on plant growth. This in turn is directly linked to the carbon cycle – and is perhaps also an interesting tangent into why the phenomenon of “carbon fertilization” may dampen some of the negative effects of increased CO₂ at least in the short-term. Trees, both during respiration and photosynthesis use “leftover” glucose molecules from both processes to build their structural components. The “traits” or morpho-physiological characteristics of plants are also used in CARAIB’s simulations, because each species behaves differently with respect to their responses to environmental factors and to their allocation of carbon molecules to leaves, roots, stems (trunk).

Each run within a CARAIB simulation grows plants, and the biogeography model captures the ecosystem dynamics, by having the plants compete for light and water. Besides the competition between the species, CARAIB also calculates other stresses, in addition to water stress, like thermal stress (i.e. temperatures beyond the thresholds for survival or even germination). These factors can lead to mortality, and possible changes in a species’ net primary productivity. Essentially, the output is what is used to create potential distributions of the species of interest. One main improvement of CARAIB simulation would be the implementation of a migration module. Indeed, in the present version, there is no dispersal limitation: all the plants to simulate are allowed to grow everywhere, or even allowed to have seeds everywhere in the selected area and the absence of one particular species only relies on the fact that its productivity is ‘very low’ or that germination criteria are not met.

In the model, the first components are “natural” processes, in the sense that prior to heavy anthropic influence, there was some dynamic equilibrium that would maintain a composition of species within a given biome. Of course, in a vegetation model with tropical species, this is still simplistic, because it is known that plant species composition is also influenced by other interactions, such as grazing and parasitism. The next module is a fire module, where natural frequency and intensity of burning events can be adapted to reflect human influence – example, slash and burn agriculture – and can heavily sway the final distribution and composition of species. This particular

module within CARAIB is especially relevant to consider management scenarios and the impacts on future distributions in areas of high-fire risk. Of course, the fire module also relies on the output from the other modules – litter (respiration), drier soils (hydrological budget), and some mechanism to light a fire (lightning, slash & burn intensity, human density and behavior) to calculate the probability of fire and its effect. It is worth noting that thus far, CARAIB has not yet used factors such as slash & burn, or human density in their fire ignition probability.

For this study, we narrowed down our choice of BAF species of interest to 94 tree species. They were selected using the same criteria described in Raghunathan et al. (2015), and even included species important to another endemic frugivorous primate in Southern Bahia, the *Sapajus xanthosternus*. As CARAIB is a grid-point model and can be run at any resolution, we ran the simulations for the entire BAF biome at 5-minute resolution. This also meant that the resulting rectangular delimiter included portions of *caatinga* and the Amazon biome. The climate data needed to run CARAIB includes: daily average air temperature; daily amplitude of air temperature (between night and day); precipitation; air relative humidity; percent of sunshine hours; wind speed. The other input for CARAIB included samples of presence data for the tree species of interest which allows to extract several climate thresholds considered as species traits.

While in Raghunathan et al. (2015) we already described the importance of using species-specific values for morpho-physiological traits, the updated values were not easily available in the literature for the species simulated here. As a result, the simulations were run using average values of Plant Functionality Types (PFTs). Ongoing research has suggested that the outputs of CARAIB are greatly improved when species-specific traits are included (Paillet 2018; François et al. 2019; Hambuckers et al. 2019; Paillet et al. 2019). The fire module was not used for this region, because fire is not a particular threat in the GHLT distribution per se. However, it may be a valuable next step in considering the role of fire particularly in the western distribution, as we move towards a drier, Atlantic-forest to *caatinga* transition ecosystem.

Maximum ENTropy: MaxENT

There have been several uses of Maximum Entropy (MaxENT) modelling to determine availability of suitable habitats for species, based on climate impacts. MaxENT uses presence only data and environmental variables (predictors, linked to the presence – climate, anthropic pressures, distribution of prey have been used in different analyses; Hernandez et al. (2008); Bouyer (2015); Collins and du Toit (2016)) to produce probabilities of distributions. MaxENT assumes that the probability is uniform over a geographic area of interest and moves away from this probability based on the constraints measured from the predictor variables. MaxENT treats background points as

“pseudo-absences”, which means that if the sampling of species distributions is biased (which is unfortunately the more common scenario), then the predicted distributions are also likely to be biased (Phillips and Dudík 2008; Merow et al. 2013). Elith et al. (2011) provides an excellent overview of MaxENT and cites in more detail the applications since MaxENT’s development in 2004. They argue that presence-only data can be modelled in a similar way to presence-absence data, but naturally imply that where presence-absence is known, they can eliminate issues in sampling bias and models using presence-absence are a better substitute. Limits of the background taken into consideration has to be set, for instance by checking the increase of fit when increasing the background extension as suggested by VanDerWal et al. (2009).

In different words, MaxENT finds the “largest spread” or maximum entropy within geographic data related to species presence, against a set of environmental variables (which are a part of the background). This procedure is similar to maximising the log-likelihood of the background data associated with presence, with a penalty. The penalty is that each environmental variable is weighted based on how much complexity it adds to the model and the sum of the weights of all the environmental variables is what determines how much the log-likelihood should be adjusted to avoid overfitting (i.e. a potential over-prediction of possible distributions; Phillips and Dudík (2008)). This process of adding the weights to calculate the penalty uses a regularisation parameter, which can be adjusted by the user.

MaxENT specializes in predictive accuracy at the cost of biological interpretation – for example, there may be a reason other than climate for a species not to be present in an area. However, several studies (Elith et al. 2006; Elith et al. 2011; Merow et al. 2013) have shown that MaxENT modelling, compared to other methods, works better, and is therefore one of the preferred analyses used for species distributions. However, studies have also shown some of the disadvantages in presence-only modelling (Gomes et al. 2018), particularly when sufficient attention isn’t paid to “commonness or rarity” of the species of interest. Liu et al. (2016) tested methods for selecting a logistic threshold and summarized the challenges with respect to adequate conservation planning: in rarer species, models tend to increase omission errors rather than commission errors, meaning that suitable locations might be left out in predictions and could be inadvertently lost to poor territorial management. For common species, the inverse is usually the case, potentially leading to poor resource allocation for conservation planning and management. Omission errors are linked to correctly predicting presence records (or “sensitivity”), while commission errors are linked to correctly predicting absences (“specificity”). Typically, sensitivity and specificity are independent of one another, but more importantly, are independent of the “prevalence” or the proportion of sites where species are considered as present (Shabani et al. 2018). This is of course valid for MaxENT or CARAIB, and we calculated these parameters for both models.

Most studies addressing climate impacts on species' distributions use bioclimatic variables, which can be available for free at worldclim.org or created in R. For this research, we calculated the bioclimatic variables from the four GCMs, for both the RCP4.5 & RCP8.5 scenarios.

A quick comparison between CARAIB & MaxENT

While this is dealt with in quite a bit of detail in the chapter, "Contrasting climate risks predicted by dynamic vegetation and ecological niche-based models applied to tree species in the Brazilian Atlantic Forest", this section provides a quick summary of the similarities and differences. Both models use presence-only data and can simulate multiple species at once. Barring that, there are few similarities between them. Perhaps the most interesting feature to explore is the relative consistency with which MaxENT produces more pessimistic outcomes under future climates, compared to CARAIB. There could be two ways approach this concern, one of which was not done in this research. Apply a different "regularization" factor in MaxENT, though this may produce more "noise", rather than appreciable differences in the gains; or, in more practical terms, apply a "precautionary principle" with respect to conservation decisions. One appreciable difference that may be considered is the relative amount of time it takes to run simulations. Because the processing (statistics, interactions) in MaxENT are much less complex relative to CARAIB, simulations on a similar geographic area, for the same number of species are appreciably quicker in MaxENT compared to CARAIB. However, at a site-level, where on-the-ground conservation measures are typically applied, CARAIB may prove more reliable precisely for its ability to simulate plant growth, and for the future opportunities to consider dispersal by fauna.

SDMs, including MaxENT predict potential ranges and merit being updated as new data are available, in terms of distribution but also with respect to any changes or updated environmental variables that may influence their distributions. The same way that CARAIB would benefit from using species specific morphological traits, both CARAIB and MaxENT could benefit from including key interactions and other biological variables, rather than focusing mostly on climate and physical variables in the environment.

We compared CARAIB and MaxENT outputs by calculating True Skill Statistic (TSS), Area under the curve (AUC), specificity, and sensitivity (Shabani et al. 2018).

Observing GHLTs in the field

This section describes the field methods, though a detailed description of the methods is provided in the chapter, "Deterministic modelling of seed dispersal based on observed behaviours of

an endemic primate in Brazil". The group I observed was one of a few being studied as part of a broader research programme that is led by the Royal Zoological Society of Antwerp (RZSA). In this thesis, the group is referred to as the "Colônia da Una" or CU group, because further on, we discuss behavioural observations obtained from other studies. The methods used to observe the group are exactly the same as those described in Catenacci et al. (2009); Oliveira et al. (2010); Cardoso et al. (2011). Two adult individuals in the group had radio collars, and using telemetry devices, we followed them from sleeping site to sleeping site (i.e. when they left their sleeping hole in the morning, until they went into the same or different one in the evening) 5 to 8 times a month. Positions were recorded every 20 minutes, and all behaviours linked to feeding, territoriality, predator presence, and resting/grooming, sleeping site use were recorded. The *Pourouma* genus fruits between October-April, and this coincides with GHLT reproductive season.

Besides collecting data on the behaviours, considerable effort was dedicated to learning about the physical and biotic environment. We established parcels throughout the seasonal home-range. These were inputs to learn more about the factors affecting GHLT trajectories, and to parametrise dispersal within their seasonal home-range. Defecated seeds were collected, and *in-situ* germination studies were conducted. Another, entirely non-conclusive study on seed predation was set-up as well. The first challenge was identifying sites within the home range where there were no *Pourouma* individuals within a 50m radius. Once we successfully identified 10 sites, a seed predation experiment was designed, with i) exposed seeds with 1 m of nylon threads attached, in an attempt to test seed removal, and ii) an "open" pile of accessible seeds. No reports were made from this experimental design, because the results were generally inconclusive. After one year of visiting the sites of the predation experiment (once a week for the first 6 months, and then once a month up to a year), the seeds were lost and untraceable, or remained in the same site, and dried, with only two "threads" that had the appearance of being gnawed. While the missing seeds may have been lost to predation or possibly secondary dispersal events, it is hard to draw any reasonable inferences. Pitfall traps for terrestrial mammals, and surveys on dung-beetles, or other secondary dispersers or predators may be interesting in this region. Culot et al. (2009) showed that *Pourouma* genus seeds have been buried or predated upon following dispersal events by *Saguinus*, although, at much lower rates compared to other tree species that were observed in that study.

In addition to the actual "data of interest", we were fortunate to observe other grooming and infant carrying behaviours. One particular event that was quite unusual was that the secondary female also gave birth, within 10 days of the alpha. How odd and exciting for two females to carry, within the same group? This is not a regularly documented incident among GHLTs. We also witnessed a blatant attempt at infanticide, during the course of an encounter, approximately three weeks following the birth of this interloper. Following ethical considerations, when the adults were directing alarm calls

towards us, as we inched away from the scene of the crime, we cut-short our observations, expecting to return the following day, to four adults and one infant. This was confirmed. When indicating that at the end of my research period, there were four adults and 02 infants, this is because GHLTs can have up to two birth events in one reproductive season. Of course, it was the alpha female who had her second infant. We would know the exact date of the birth, because one day, four adults and a juvenile were left at their sleeping site, and the next, a little tail was dangling off the mother's back.

Perhaps the biggest gap in terms of data not-collected is linked to lack of a comprehensive phenology study, that would run for at least a few consecutive years. This is because the site was a new site. The RZSA, with a broad research focus on, "What happens to GHLTs in degraded areas with anthropic presence" moved out of the environs of the Una Biological Reserve to improve understanding on the minimum necessary conditions for GHLT survival. The phenology study was being set-up at the same time as this research started, so even one year's data would not be available in time. Informally, as I would stalk my group, it was interesting to note that during the few weeks where my feeding behaviours would only have *Pourouma* and *Artocarpus* in the observations, the forest did seem "empty". What would happen if the jackfruit weren't in the habitat? Would a few weeks of dieting on *Pourouma* alone suffice? A confounding variable is that we couldn't know whether the group spent so much time hiding in liana conglomerates to search for food (insects, small amphibians or small reptiles), or were they resting due to the charges of infant-rearing? The faecal samples did not usually have telling signs of undigested insect material that could sometimes appear. But a genetic study, as conducted by Oliveira during his field work (*pers. communication*) where he sent faecal samples to be analysed, would have been an interesting (though expensive) addition.

What is perhaps always missing in professional descriptions of methods descriptions is the rich complement of "data" that is perceived without being used. In this field site, we were fortunate to have observed, sometimes only briefly, sloths, toucanets, tayras, kinkajous, hawks, various snake species (including one potentially mimicking the coral snake), and my field assistant (who had previously worked with *Sapajus xanthosternus* for 10+ years) confirmed that he heard vocalisations of the capuchins one morning. Additionally, the few evenings when the GHLTs were late arrivals to their sleeping sites, bats (unrecognisable to me at species level) were also seen flying around the trees. It was also always amusing to see beautifully intricate little frogs jumping up from puddles after rainy evenings. While defaunation and degradation are problems and must be confronted, it can be hopeful to know that even these areas can be home to the intrepid, beautiful, slithery, diversity that makes the BAF the hotspot it is.

3 Contrasting climate risks predicted by dynamic vegetation and ecological niche-based models applied to tree species in the Brazilian Atlantic Forest

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Abstract

Climate change is a threat to natural ecosystems. To evaluate this threat and, where possible, respond, it is useful to understand the potential impacts climate change could have on species' distributions, phenology, and productivity. Here, we compare future-scenario outcomes between a Dynamic Vegetation Model (DVM; CARAIB) and an Ecological Niche-based Model (ENM; MaxENT) to outline the risks to tree species in the Brazilian Atlantic Forest, comprising the habitats of several endemic species, including the endangered primate *Leontopithecus chrysomelas* (Golden-Headed Lion Tamarin; GHLT), our species of interest. Compared to MaxENT, the DVM predicts larger present-day species ranges. Conversely, MaxENT ranges are closer to sampled distributions of the realized niches. MaxENT results for two future scenarios in four general circulation models suggest that up to 75% of the species risk losing more than half of their original distribution. CARAIB simulations are more optimistic in scenarios with and without accounting for potential plant-physiological effects of increased CO₂, with less than 10% of the species losing more than 50% of their range. Potential gains in distribution outside the original area do not necessarily diminish risks to species, as the potential new zones may not be easy to colonise. It will also depend on the tree species' dispersal ability. So far, within the current range of *L. chrysomelas*, CARAIB continues to predict persistence of most resource trees, while MaxENT predicts the loss of up to 19 species out of the 59 simulated. This research highlights the importance of choosing the appropriate modelling approach and interpretation of results to understand key processes.

Keywords

Climate change, dynamic vegetation model, primates, *Leontopithecus chrysomelas*, tree species distributions

Introduction

Climate change is a threat to natural ecosystems. In order to adequately evaluate this threat and, where possible, respond, it is useful to understand the potential impacts climate change could have on species' distributions, phenology and productivity. The Brazilian Atlantic Forest (BAF), our area of interest, is a biodiversity hotspot (Myers et al. 2000; Mittermeier et al. 2005), with many endemic plant and animal species, forming complex communities of inter-dependent organisms, that may succumb to climate risks.

Traditionally, conservation practitioners and ecologists use ecological niche-based models (ENMs), also called species distributions models, to identify climatically appropriate regions for the species in the future (Elith and Leathwick 2009). Examples of such models are MaxENT (Maximum Entropy Model; Elith et al. (2011)), GARP (General Algorithmic Rule-set Production; Townsend Peterson et al. (2007)), or logistic models (see Annex Table 3.1 and text for data needed with ENMs). Typically, these models identify empirical relationships between values of environmental (or predictor) variables for known species locations. These relationships are used to predict the likelihood of presence, across an area of interest and allow us to infer for future (or past) areas under other conditions. Their main advantage is simplicity of use, but they can be quite limited. Also, different ENMs could produce different results, despite modelling the same species and the same zones. Usually the ENMs do not include or control important physiological phenomena such as short-term acclimation, or genetic adaptation (Smith and Dukes 2013). While they simulate the niche, including biotic interactions, they have to rely on the assumption that these interactions will not change when projecting with new climate data, while these interactions and their evolution are important factors governing species ranges (Brooker et al. 2007). Climate ENMs work with plants (Carnaval and Moritz 2008; Colombo and Joly 2010; Franklin et al. 2013; Khanum et al. 2013) but also with animal (e.g. Collins and du Toit (2016) *Bunolagost monticularis*; Vasconcelos et al. (2012) with terrestrial reptiles; Carolan et al. (2014) with hemipteran insects). Process-based dynamic vegetation models (DVMs) are apt tools to study impacts of climate change on vegetation (Dury et al. 2011; Snell et al. 2014) and may be better suited than ENMs. As DVMs simulate the growth of plants, based on plant functional types (Sitch et al. 2003) or biological affinity groups (Laurent et al. 2004), they enable researchers to monitor plant responses to changing environments (see Annex Table 3.1 and text for data needed with DVMs). ENMs and DVMs allow for simulating several species at once, while DVMs also include species interactions (resource competition). Process based modelling is less developed for animals, with fewer studies demonstrating this approach (Boyles et al. 2011). Few studies on climate impacts on animals have incorporated the physiological responses (Kearney and Porter 2009), possibly because the physiology of mammals and their competition may be harder to simulate. Additionally,

process-based modelling (plant or animal) is sometimes more time consuming, particularly with respect to the level of data required (for instance with trait data) and computation time.

In the tropics, vegetation depends on frugivorous fauna, as much as the animals rely on plants. 80–90% of animal biomass corresponds to frugivores (Fleming et al. 1987; Estrada et al. 1993), while climax forests host a majority of zoolochorous tree species, i.e. vegetation reliant on frugivorous fauna for seed dispersal (Peres and Roosmalen 2002). Simulating climate change impacts on each component of the BAF biome is difficult. This is due to the large diversity of species (and corresponding lack of uniform spatial and trait data) with different degrees of socio-economic and ecological importance. However, we can still gather useful information while prioritising some species (flora or fauna) characterized by defined criteria. The threat of extinction could represent one of these criteria because threatened species are more sensitive to the degradation of their ecological niche than the other species. Here, the tree species selected to understand the potential climate risks, are those known to be important, as a food or sleeping site source, to an endangered frugivorous primate, *Leontopithecus chrysomelas* or Golden-Headed Lion Tamarin (GHLT). The GHLTs have a small area of occurrence, decreasing due to habitat loss, in northeast Brazil, principally in southern Bahia. With such range restriction, it may be hard to know whether the small range is a consequence of climatic conditions, geographic barriers, or other reasons. Therefore, modelling the response of tree species important to GHLTs in terms of habitat and food resources may be more useful than trying to build a climate ENM of the monkeys.

There is mounting evidence that climate change will have impacts on several species. Thomas et al. (2004) used a species-area approach to understand the extinction risks of various taxa, under the face of climate change, and projected that 20 – 45% of species (overall) could be extinct under a mid-range climate scenario, with and without dispersal. Root et al. (2003) and Thomas (2010) conducted meta-analyses that showed temperature related shifts in 68% of considered species, that are also consistent with their physiology. Monzón et al. (2011) provided several case studies from different ecosystem types, where climate-induced range shifts led to species moving outside of protected areas, thereby increasing their vulnerability to extinction. Otherwise, evidences of population expansion at the leading ‘cold’ edge are much more frequent than proofs of retreat at the ‘warmer’ trailing edges (Thomas 2010). The BAF biome is already threatened with heavy fragmentation, with only 8% of the original forest cover remaining (Myers et al. 2000). In the GHLT distribution, there is only one major protected area (Una Biological Reserve), and much of the GHLT habitat is converted to agro-forestry systems for cacao production. Climate change can therefore exacerbate the impact of fragmentation, as well as threaten the BAF vegetation. Conversely, with much of the BAF biome lacking larger-bodied frugivores due to hunting, GHLTs may play an important role in habitat maintenance, though it may not functionally replace the losses.

In Raghunathan et al. (2015), we found with the CARAIB DVM that the potential future distributions of various BAF tree species may be limited by soil water availability in the future. However, under the pessimistic A2 climate scenario, the model projected significant range reduction compared to the present-day for only three out of the 75 studied species, with no important losses in the B1 and A1B scenarios. These DVM results were considerably optimistic compared to those of Colombo and Joly (2010), who ran two ENMs (MaxENT and GARP) for 33 BAF species and obtained significant range loss in future predictions. Also in Raghunathan et al. (2015), we ran steady-state simulations with average climatological data, and identified the need to conduct fully transient simulations. In a transient simulation, the weather changes each year, and the reaction times of vegetation may not be quick enough to respond to climate change, therefore incurring higher risks of extreme climate events. We also stressed the value of using a range of general climate circulation models (GCMs) to account for the differences in projected future climates. In addition, few studies have conducted process-based simulations for vegetation on the many species in this region, and fewer have compared different methods. Here, we compare the outcomes between a DVM (CARAIB; CARbon Assimilation In the Biosphere; Francois et al. 1998; François et al. 2006; Dury et al. 2011) and an ENM (MaxENT; Phillips and Dudík 2008) driven by climate predictions of a range of GCMs under two Intergovernmental Panel on Climate Change Assessment Report 5 (IPCC AR-5) representative concentration pathways (RCP) to outline the range of risks to BAF tree species, and consequently the GHLTs or sympatric fauna, in the future climate.

Methods

Climate data and species distributions

The monthly climatic fields required to run CARAIB are the mean surface air temperature, diurnal temperature range, precipitation, wind speed, relative sunshine hours and air relative humidity. The present-day temperature (minimum, average and maximum) and precipitation variables were obtained from WorldClim version 1.4 (www.worldclim.org). These monthly mean data, representative of 1951-2000 period, with a spatial resolution of 30 arcseconds (about 1 km²) were compared to observed temperature and precipitation from meteorological stations in the BAF zone and were estimated concordant (<5% difference in mean values). For CARAIB transient simulations, present inter-annual variability was derived from 0.5° Climatic Research Unit TS 3.0 dataset, also used to get the other climatic fields absent in WorldClim. For the future (until 2100), several IPCC CMIP5 GCMs (Coupled Model Intercomparison Project - Phase 5; Taylor et al. 2012) were selected for the quality of their reconstructed climate over BAF for historical period or for the extreme temperature and precipitation changes they projected for the end of the century. We classified the outputs of 33 CMIP5

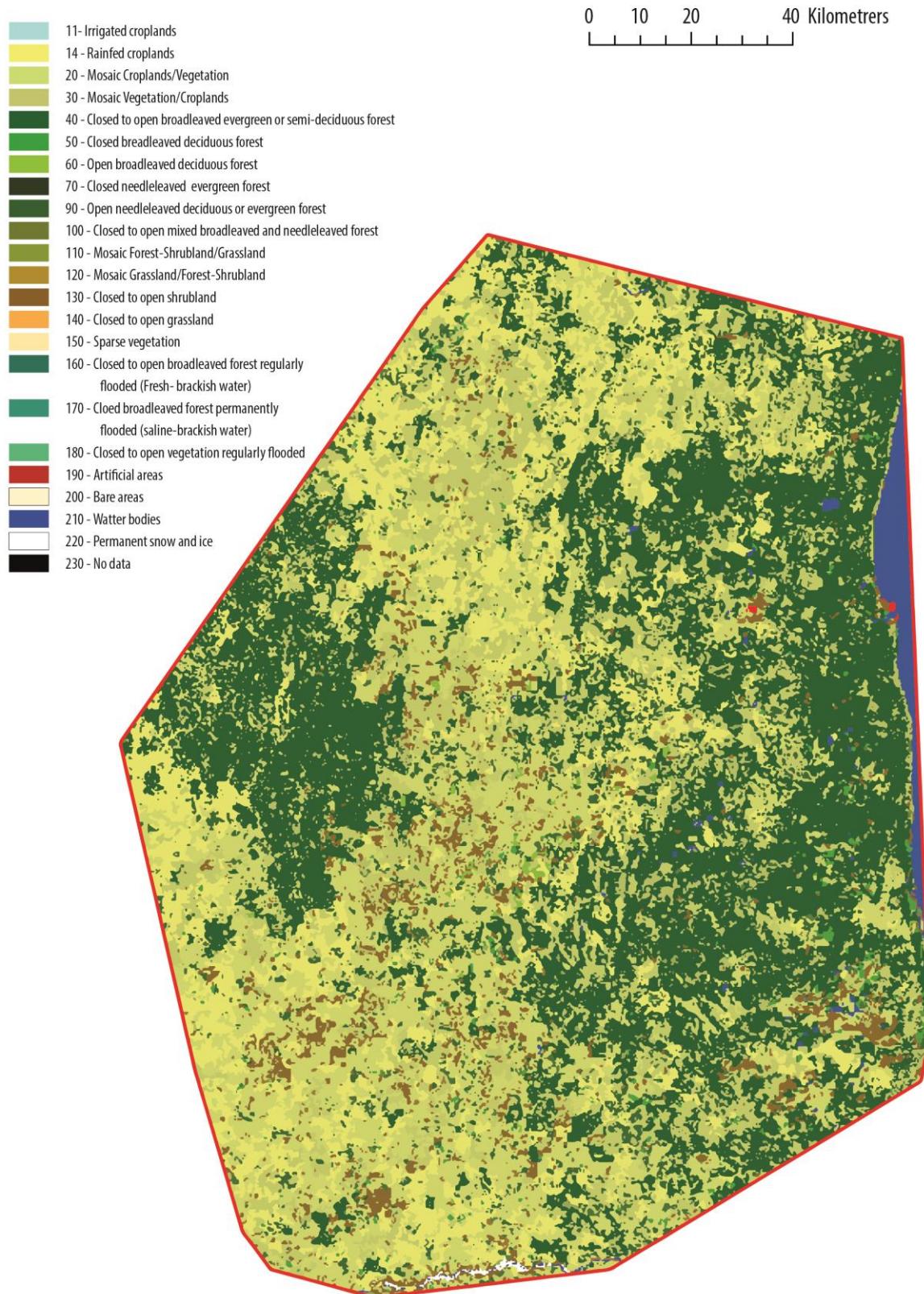
GCMs, interpolated to a 0.5° regular grid, according to their ability to reproduce present-day monthly mean temperature and precipitation from Climate Research Unit (CRU) dataset (version CRU TS v.3.21; <https://crudata.uea.ac.uk/cru/data/hrg/>). We used CRU time series for the model selection because of its spatial resolution closer to the coarse GCM resolutions and to be able to control the GCM inter-annual variability. We evaluated the mean, inter-annual variability and trend over the 1980-1999 of modelled annual and seasonal temperature and precipitation in terms of their correlations (coefficient correlation) and differences (root-mean-square error) with CRU data. Taylor diagrams (Taylor 2001) (See Annex Fig. 3.1 and Fig. 3.2) that provide a concise statistical summary of how well models match observations in terms of their correlation, their root-mean-square difference (RMSE) and the ratio of their variances, are presented in the Annex (RMS and standard deviation were normalized). Following these criteria, the vegetation model was driven by four climatic scenarios: HadGEM2-AO (highest concordance with present day values and also projecting the largest temperature rise), ACCESS1-0 (ranked 2nd and projecting intermediate climate changes), CNRM-CM5 (ranked 13th and projecting the largest increase in precipitation and the lowest increase in temperature), and CSIRO_Mk3_6_0 (ranked 32nd and projecting the largest reduction in precipitation). The GCM outputs were interpolated to 5-minute resolution and bias-corrected, to correspond to WorldClim mean reference (temperature and precipitation) and to CRU for the variables unavailable in WorldClim. The 19 bioclimatic variables necessary to MaxENT modelling were derived from these climatic projections following WorldClim definitions (Annex Table 3.2). Two different scenarios of greenhouse gas forcing (Moss et al. 2010) were used for CARAIB simulations: the RCP4.5 and RCP8.5 scenarios. They represent 4.5 W/m² (~ 538 ppmv of CO₂) and 8.5 W/m² (~936 ppmv of CO₂) of greenhouse gas radiative forcing at the end of the 21st century respectively relative to pre-industrial levels.

In addition to the 75 tree species cited in Raghunathan et al. (2015), 19 other tree species found in the GHLT habitat were added to the list (Annex Table 3.3). Several other BAF frugivores also consume these resources. The occurrence data were obtained from the same sources cited in Raghunathan et al. (2015), using the Tropics online database (www.tropicos.com). Of the non-endemic tree species many are also present in the Amazon region, and Central American forests. The high levels of fragmentation demonstrate the potential challenges of species migration and anthropogenic impacts (Fig. 3.1 & 3.2).

**Figure 3.1 Land cover image of parts of Central-South America, corresponding to area simulated with MaxENT, obtained from GlobCover 2009 Project, published December 2010
http://dup.esrin.esa.int/page_globcover.php. Red outline shows distribution of *Leontopithecus chrysomelas*. © ESA 2010 and UCLouvain**



Figure 3.2 Land-cover in *Leontopithecus chrysomelas* distribution: level of connectivity of forest area is sparse, potentially serving as a barrier to species colonisation in future climates. Same data source as Figure 3.1. © ESA 2010 and UCLouvain



Modelling

MaxENT generates species distribution probabilities over a number of sites (Phillips and Dudík 2008). Review of ENMs conclude that MaxENT often surpassed other models (Elith et al. 2006; Elith et al. 2011; Merow et al. 2013), particularly for predicting known distributions, though all models have specific advantages and disadvantages and could also surpass MaxENT (Bedia et al. 2011). Merow et al. (2013) also cited MaxENT's user-friendly interface as a key aspect of its success. We used the version 3.3.3a from the open-source archive MaxENT.jar v. 3.3.3a available at www.cs.princeton.edu/~schapire/MaxENT. Modelling was only conducted with non-endemic species (59 out of 94) for which we had at least 15 presence points, at a 5-minute resolution. We selected auto-features option and obtained a logistic output. The geographic zone for the simulations covered most of Central and South America, 87° W to 35°W and 15°N to 30°S, though the area of interest is the BAF. MaxENT outputs were generated using the following standards: Convergence Threshold: 0.00001; Maximum Iterations: 500; Auto-features: yes; Regularisation multiplier: 1. Simulations were run for a zone larger than the BAF, to encompass the overall distribution of the different species, but analyses were done only on the area of interest.

The CARAIB model was first developed with the objective to estimate the role of vegetation in the carbon cycle at global scale (Warnant et al. 1994; Gérard et al. 1999). Further, it was used to determine the potential vegetation distribution under past climates (e.g. François et al. (2006); Henrot et al. (2010); François et al. (2011)) and to simulate potential vegetation and wild fires in the future in Europe (Dury et al. 2011). In the Neotropics, CARAIB simulations of species growth provides rather consistent results in terms of present-day distribution (Raghunathan et al. 2015). Detailed descriptions of the model are given in Otto et al. (2002); François et al. (2011); Dury (2015). We used the same species occurrence datasets for CARAIB as for MaxENT but modelled the 94 species. Threshold values controlling germination and mortality under stress conditions are extracted from prescribed percentiles in their actual climate distribution extracted from the occurrence samples (not limited to South America), according to the method described in Laurent et al. (2008) and François et al. (2011). CARAIB species' distributions are principally controlled by climate thresholds, while their productivity is also dependent on the morpho-physiological traits. In the absence of specific species traits, we used plant functional type values (Annex Table 3.4). The simulations were run from 1901 to 2100 with transient climate and atmospheric CO₂ concentration evolving according to the selected RCP scenarios. We also tested the effect of a constant CO₂ at 350 ppm.

Modelling validation and comparisons

Simulations with MaxENT and CARAIB were validated by testing the level of overlap between the simulated present-day distributions and the known occurrences over the South America, up to 30 ° S. We produced maps and also used 4 agreement criteria (Allouche et al. 2006): Area under the ROC curve (AUC), true skill statistic (TSS), sensitivity (Se, proportion of presence data points correctly predicted by the model) and specificity (Sp, proportion of absence data point correctly predicted by the model). AUC and TSS take into account a set of both presence and absence data points; TSS, Se and Sp are threshold dependent. As absence data, we generated pseudo-absences at random in 1,200 km buffers around the presence data points, keeping the total number of pseudo-absences equal to that of presences. The buffer radius was selected after preliminary investigations with an ENM, following the method of VanDerWal et al. (2009) which consists of generating pseudo-absences not too far from the presences (this was an independent procedure of the modelling). As threshold, we used the equal sensitivity and specificity logistic threshold given in the standard output of MaxENT, which is one of the common methods to fix a logistic threshold. For CARAIB, we used a fixed net primary production (NPP) threshold of 150 g C m⁻² yr⁻¹, despite the fact that this value may vary among the species according to their performance and biotic environment. Indeed, no field values are available to infer such thresholds, while using the occurrence data and a set of pseudo-absences to optimize the selection of thresholds would seem tautological. Prediction at random may provide AUC of 0.5. Commonly, values larger than 0.7 let suppose acceptable agreement, while values between 0.8 and 1 are considered as good to excellent. These reference values can be also considered for Se and Sp. TSS varies between -1 and +1, negative values indicating a level of agreement no better than random. According to Landis and Koch (1977), kappa between 0.4 and 0.61 indicate moderate agreement, with kappa above 0.81 indicating almost perfect agreement. These values can be used also for TSS since it varies accordingly and equals kappa when the numbers of presence and absence are the same. To compare future simulations with present, we used the same thresholds as for the present.

Results

Species modelling validation and comparison MaxENT-CARAIB

For MaxENT models, most of the agreement indicators showed at least acceptable agreement with good to excellent agreement for most of the 59 simulated species (Fig. 3.3 & Annex Table 3.3 for Se, Sp, TSS & AUC values). This suggests that the predicted distributions for the present-day climate are concordant with known distributions. CARAIB, gave indicators with lower AUC, TSS and particularly for Sp while Se was higher (Annex Table 3.3). The comparison for MaxENT and CARAIB of the same 59 species over South America shows that the predicted areas were not fully overlapping, as exemplified in Fig. 3.5 (and Annex Fig. 3.4 for CARAIB simulations without accounting for potential physiological effects of CO₂ fertilisation), for three species. In general, CARAIB seems to predict larger ranges than MaxENT, in particular, it tends to expand the range of many species, for instance over the Amazon even when no occurrence data were available over this area. This explains why Sp was lower and Se was higher for CARAIB (Annex Table 3.3).

Climate change

In the RCP8.5 scenario, which is the most pessimistic, the average annual temperature increase is ~3°C along the coast, with a progressively bigger difference between present day and future climates as we move inland, with CNRM_CM5 showing the least warming, and ACCESS1_0 and HadGEM2_AO higher increases (Fig. 3.4a). In the GHLT range, all but CNRM_CM5 show between ~7 to 10% decrease in average annual precipitation (present-day average annual precipitation is ~2000mm in the GHLT's distribution), while the four GCMs predict precipitation increases in the southern part of the BAF zone (Fig. 3.4b). Differences in future soil water levels calculated by CARAIB for each GCM follow the predicted changes in precipitation, with areas that experience loss in precipitation potentially losing 20 to 30% of the original soil water levels (Fig. 3.4c). The RCP4.5 scenario predictions are slightly more optimistic, with average temperature predicted to increase by 2°C, about ~7% less precipitation in the GHLT distribution, and up to 10% decrease in soil water compared to the present-day (Annex Fig. 3.3).

Species future ranges

With the MaxENT simulations for the future, all the GCMs predicted range losses compared to the predicted present-day distribution in both scenarios (Fig. 3.5 & Fig. 3.6, Annex Fig. 3.4). In the RCP8.5 scenario simulations, ACCESS1_0 predicted 100% range loss in three species (*Cheiloclinium cognatum*, *Macoubea guianensis*, and, *Pourouma mollis*) – BIOCLIM variables with highest impacts were temperature seasonality and precipitation in the driest quarter in ACCESS1_0 – while in all four

GCMs, more than half the species had a predicted loss greater than 50% of their originally predicted distribution (Fig. 3.6a). CARAIB's projections for the future, with increasing CO₂, are consistently more optimistic in terms of losses of ranges (Fig. 3.6b). Only the HadGEM2_AO GCM had a predicted loss of almost 50% of its current-day distribution for one species (*Manilkara maxima*). In the CARAIB simulations without CO₂ fertilisation, the predicted losses were more important, with HadGEM2_AO showing more than 50% loss in original distribution for 15 species, and ACCESS1_0 for 1 species (*Campomanesia dichotoma*, Fig. 3.6c). MaxENT simulations show gains in potential distribution, compared to the original area (Fig. 3.7a), with substantial number of species doubling their potential area of distribution in the future scenarios in each GCM. The range gains were more important with CARAIB (Fig. 3.7b). The more optimistic predictions in CARAIB may be due in part to CO₂ fertilisation. The proportionately lower levels of gains and losses are consistent with the known effects of CO₂ fertilisation on plant growth. Zooming into the GHLT distribution, CARAIB almost consistently predicts presence in the present-day simulations, and in the future, while in MaxENT, several species risk extinction. Particularly, for the RCP 8.5 scenario simulations in MaxENT, the ACCESS1_0 GCM is most pessimistic with 19 species disappearing from the GHLT range, and 8 – 10 species disappearing with the other three GCMs. The RCP 4.5 scenario simulations in MaxENT are similarly pessimistic with ACCESS1_0, with up to 16 species disappearing from the GHLT range, and 3 to 5 species with the other GCMs (Annex Fig. 3.6a and Fig. 3.7a). The RCP4.5 scenario simulations for CARAIB with and without CO₂ fertilisation remain more optimistic than MaxENT, both in terms of numbers of losses and predicted gains (Annex Fig. 3.6b, 3.6c and Fig. 3.7a, 3.7b).

Figure 3.3 Differences between a) specificity, b) sensitivity, c) TSS, and d) AUC between CARAIB and MaxENT, only for the 59 species simulated in both models.

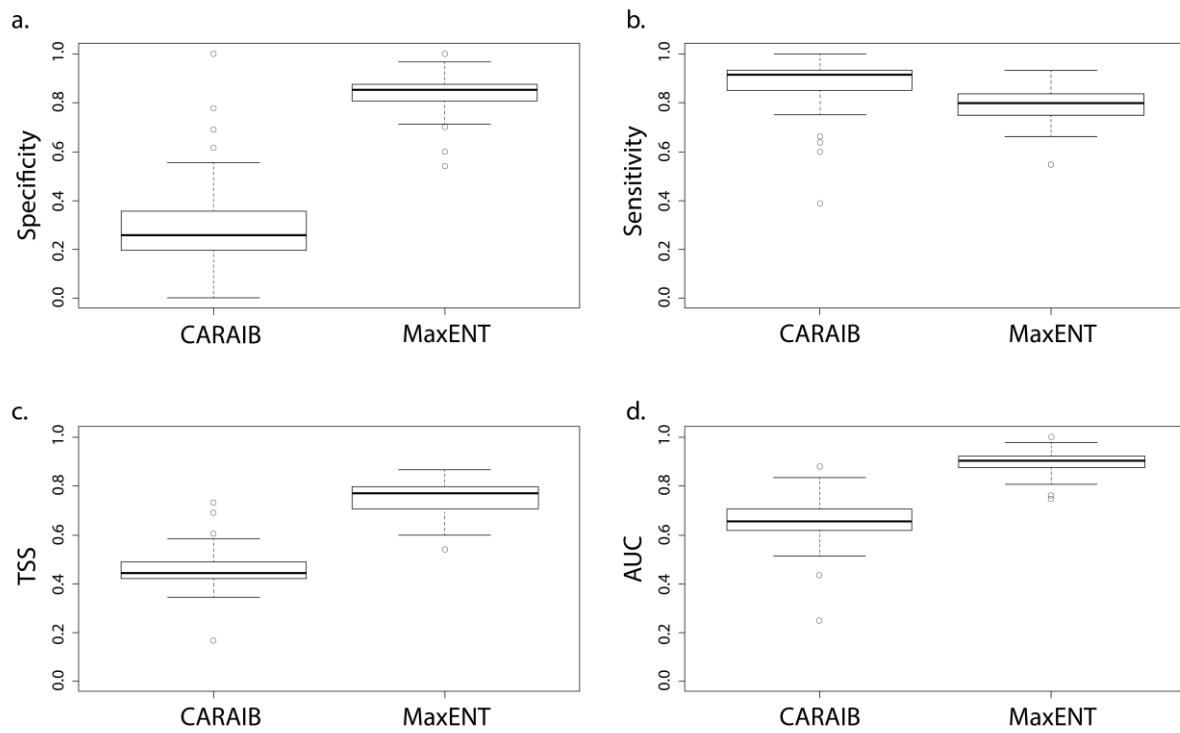
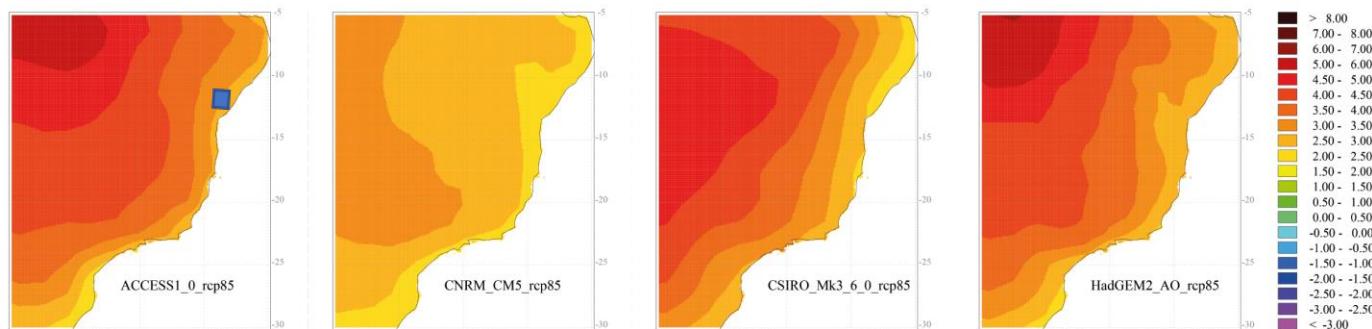
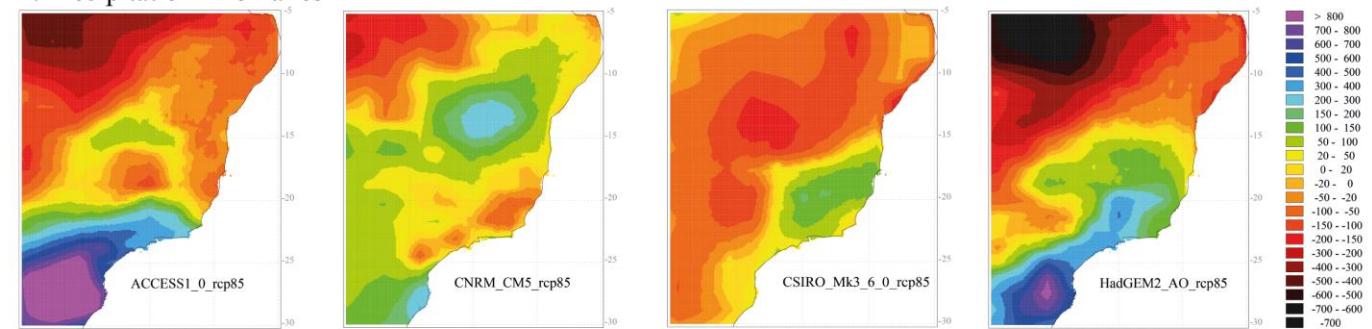


Figure 3.4 Annual mean temperature anomalies °C (a), annual precipitation anomalies mm/year (b), increase factor of soil water availability anomalies, in relative units (SW-WP/ FC-WP; SW soil water, WP wilting point, FC field capacity) (c) between present-day simulation and RCP8.5 scenario for 4 GCMs. The blue square in ACCESS1_0 RCP8.5 temperature anomaly shows the approximate *L. chrysomelas* distribution (41° W to 39° W and from 14° S to 16° S)

A. Temperature Anomalies



B. Precipitation Anomalies



C. Increase factor of soil water

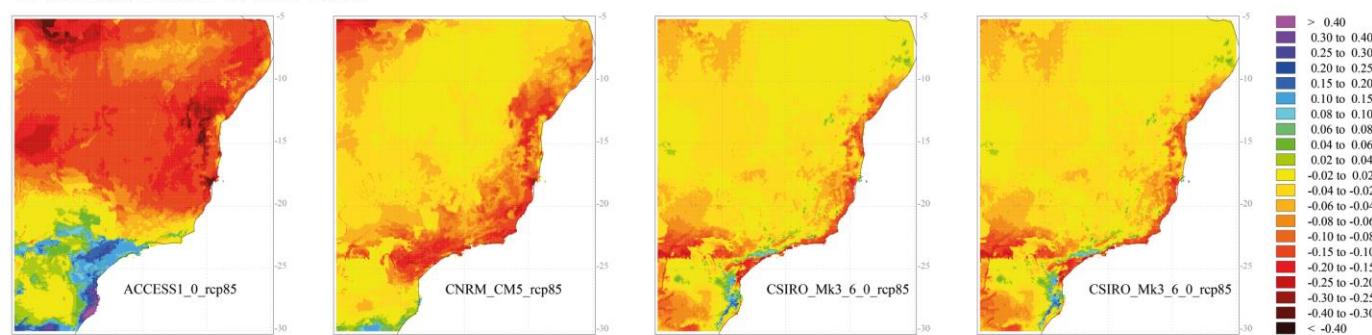


Figure 3.5 Comparison of changes in potential distributions between future and present-day simulations for 3 species between MaxENT & CARAIB in RCP8.5 ACCESS1_0 GCM simulated climate. Grey indicates areas where species was not predicted in the present-day nor future; light green areas are where the species was predicted in the present-day and in the future (i.e. grey + light green = no change); dark green areas are potential new sites to colonise (i.e. only distributed in future scenarios); red indicates areas where original predicted distribution is lost in the future. Yellow points are “current-day occurrences”

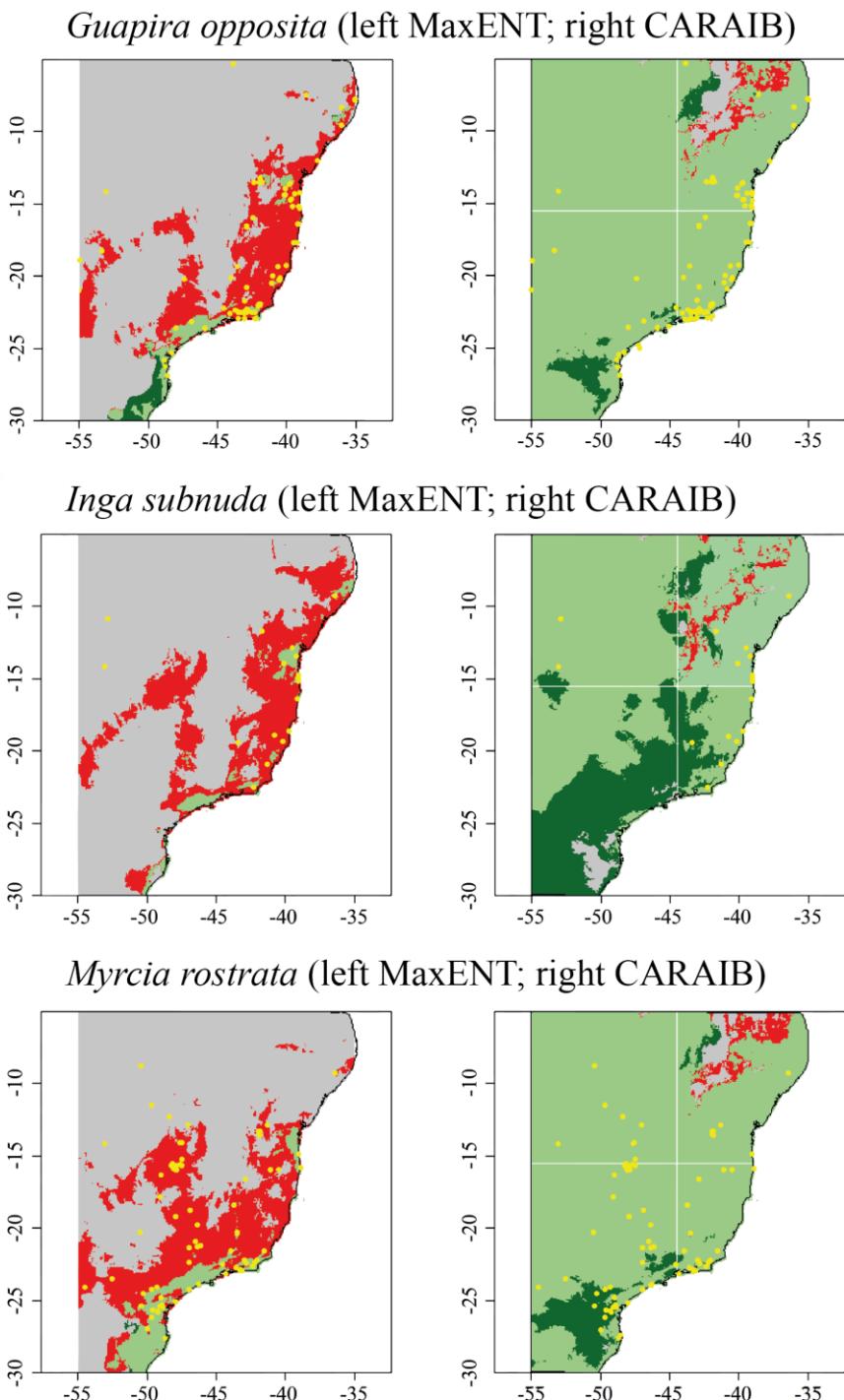


Figure 3.6 Percent loss of potential original distributions a. MaxENT, b. CARAIB, c. CARAIB without CO₂ fertilisation in RCP8.5 scenario

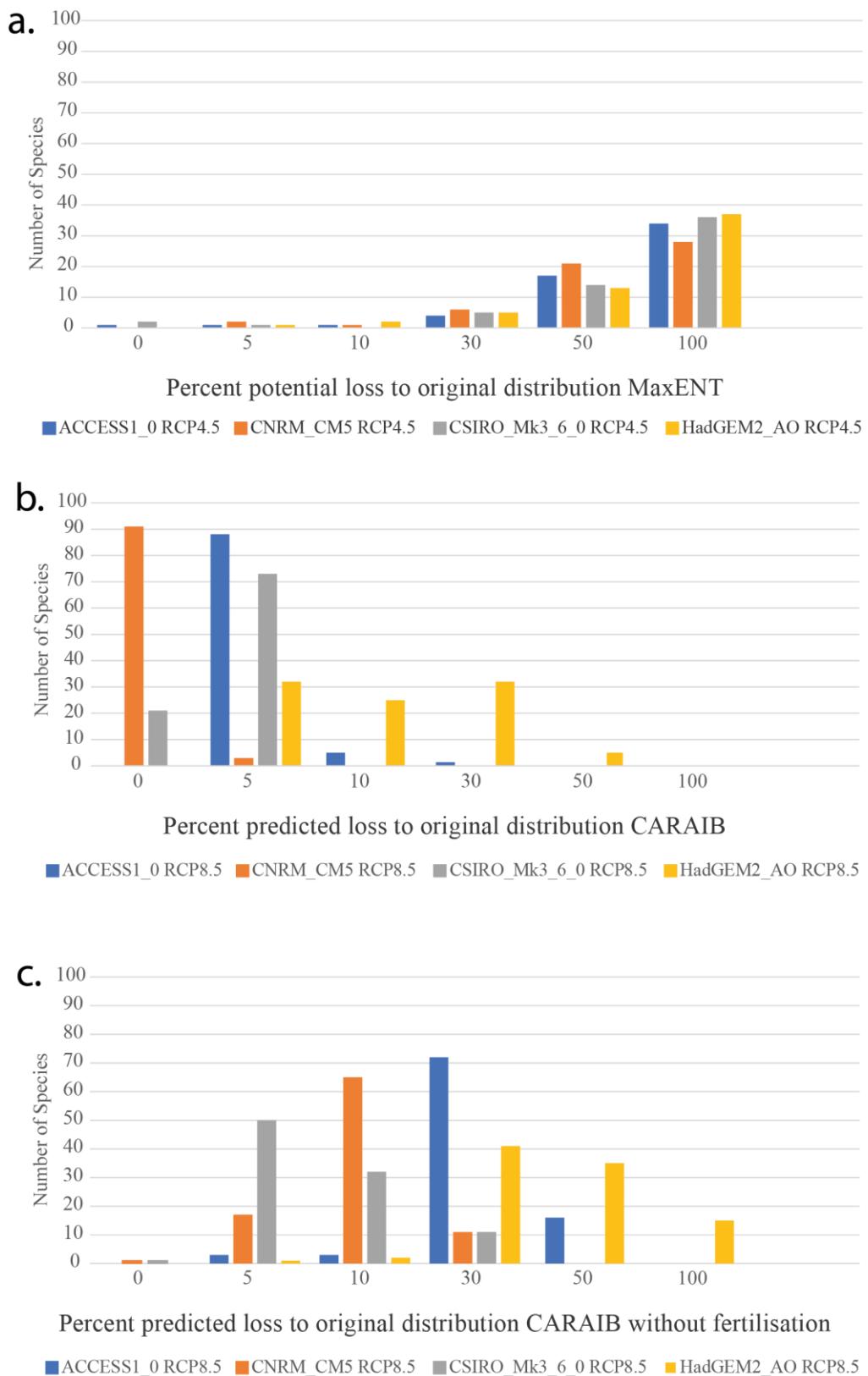
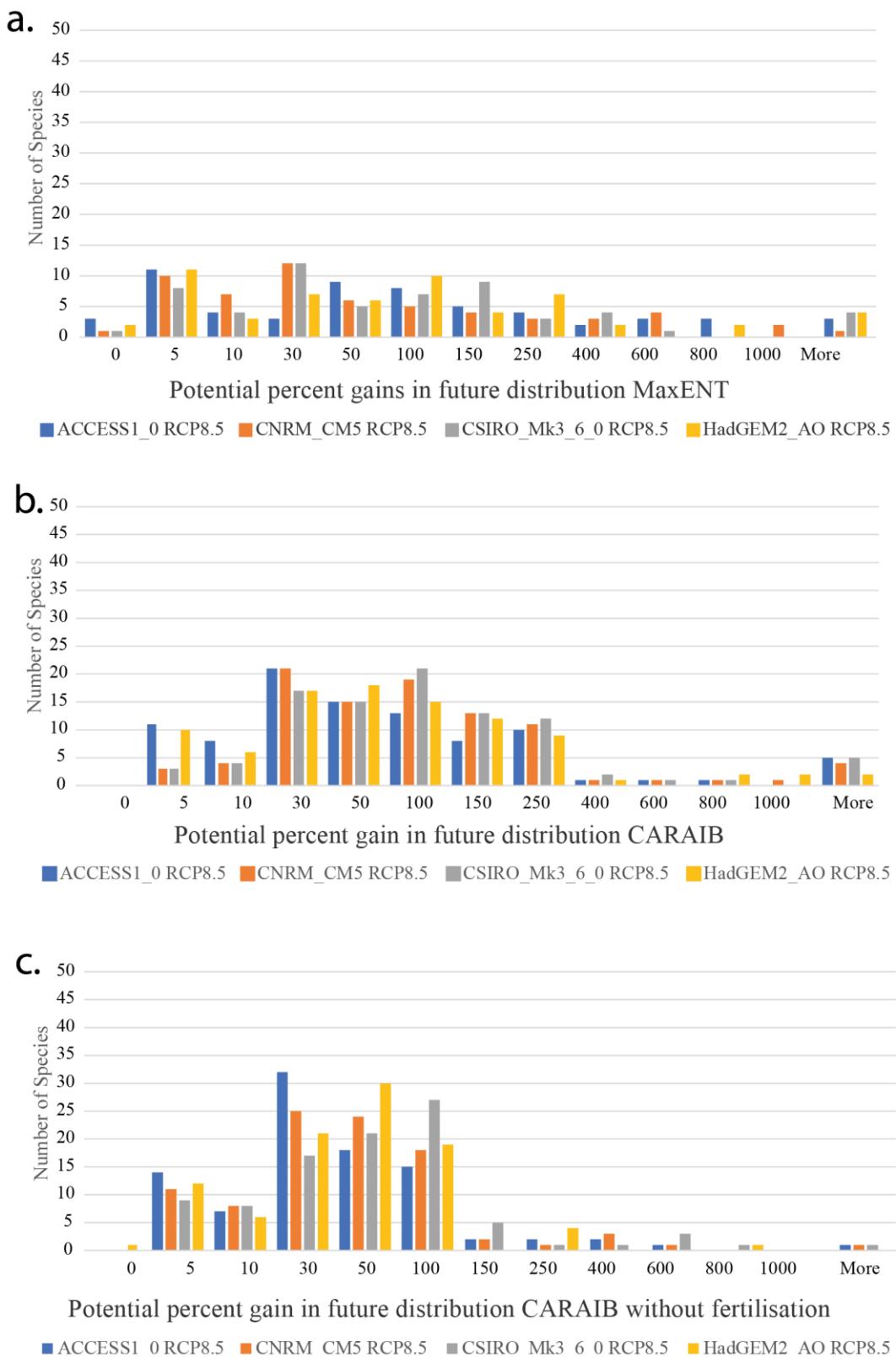


Figure 3.7 Percent gain in potential future distributions in a. MaxENT, b. CARAIB, c. CARAIB without CO₂ fertilisation in RCP8.5 scenario



Discussion

Annual mean temperature anomalies for the BAF area suggests that in the future, temperature increases may be limited to approximately 2°C in the RCP 4.5 scenarios, and between 2° and 3°C in the RCP 8.5 scenarios. Precipitation appears to decrease by up to 150 mm/month in the driest months in the northern part of the BAF, while the southern part seems to have an increase in precipitation in both scenarios for each GCM. The increased temperature appears to be consistent with other predictions for S. America as a whole. Williams and Jackson (2007) suggested that S. America is one of the regions likely to experience a “climate mismatch”, thereby producing novel climates and novel communities. This suggests that even if the plant physiology of a given species is less perturbed by an overall average increase in temperature, the combination of the increased temperatures and potential difference in precipitation seasonality could lead to drastic changes in the communities. In addition, changes in fire intensity and frequency could become an issue although much of the today fires seems linked with human activities and land conversion (de Araújo et al. 2012). In Gonzalez et al. (2010), results from dynamic global vegetation modelling using three GCMs suggested that tropical evergreen broadleaf forests were less vulnerable in future climate scenarios, compared to other regions.

Our results from MaxENT simulations for the 2 scenarios in the 4 GCMs suggest that many species risk losing more than half of their original distribution in the future, though several also have gains in the potential future distribution, outside of their original range. The CARAIB simulations for the same scenarios and models are more optimistic under a CO₂ fertilisation scenario, compared to no fertilisation, however the differences do not appear to be drastic, with CO₂ fertilisation. Only one GCM (HadGEM2_AO) had one species with more than 50% loss in the original distribution. The gains under a CO₂ fertilisation scenario were higher, with more than half of the species showing at least 30% increase in potential distributions, compared to less than half of the species in a scenario without CO₂ fertilisation. This is consistent with Cramer et al. (2001), where the simulations from 6 DGVMs suggested an overall increase in net ecosystem production with increasing CO₂. It is also consistent with Hickler et al. (2015), who demonstrated that NPP can increase due to increased CO₂ in their free-air carbon dioxide enrichment experiments. Similar results were reported from the Amazon region in Rammig et al. (2010). Within the GHLT range more specifically, the CARAIB simulations are still more optimistic compared to the MaxENT.

We supposed that the dramatic differences in the results between CARAIB and MaxENT is a consequence of the fundamental difference between both modelling strategies. The ENM identifies and uses as model a sets of suitable climate conditions in which each species occurs, corresponding at best to the realized climate niche (Guisan and Thuiller 2005). However, this procedure is unable to take into account suitable climate conditions where the species are rarely present, for instance owing to biotic interactions

because their frequency in the dataset is too low to influence the result. The DVMs have also to derive climate information from the datasets but the procedure concentrates on the extreme values in temperature, heat and water availability. These values only act as thresholds which induce mortality episodes reducing biomass. In addition, the simulation of growth in the DVMs also limits the species ranges. Indeed, to be present, a species may reach a minimum NPP value, because there occurs competition for water and light between the species pooled in the same simulation. Thus, rather than being fitted on the core of the climate data as in the ENM, the DVM captures more of the fundamental climate niche of the species and tends to overestimate the present-day range.

What is currently observed in some undisturbed places is rather enrichment of the fauna and flora (e.g. Walther et al. 2005; Steinbauer et al. 2018). This, nevertheless, should ultimately result in new equilibria between species and indubitably in species loss in the initial communities through the mechanisms of species interactions (Walther 2010). Here, it is tempting to consider that the DVM provides more consistent results than MaxENT because it better conserves the initial areas. Nevertheless, we stressed that both approaches are unable to give information (1) on what might happen inside the conserved initial (possibly overestimated) areas where new species arrive, and (2) whether the species are able to reach the predicted new suitable areas. Indeed, ENMs suppose that all the effect of factors influencing the range but not taken into account (at least biotic interaction and air CO₂ concentration) play negligible roles. The DVM tells nothing about biotic interactions (except competition for water and light) and both approaches ignore the migration processes.

There appear to be three factors that will influence species' reactions to climate change: The spatio-temporal changes (flux) in the environmental variables that limit a geographic or local distribution of a species (Helmuth et al. 2005), the ability (physiological) of a species to endure or recover from environmental stress over time (Deutsch et al. 2008); and the varying weather patterns resulting from climate change (Helmuth et al. 2005). These can determine the vulnerability of a species to climate change. Increased CO₂ can lead to higher productivity in plants, however, this is not a guarantee that they can colonise areas with appropriate climatic conditions, and the productivity may also be limited by nitrogen, phosphorous, or water, despite increased CO₂ (Cleveland et al. 2011; Reich et al. 2014). Indeed, Pan et al. (2014) suggests that under a CO₂ fertilisation scenario, global NPP might increase by 12 to 13% and begin declining or stabilising from the 2070s onwards, due to CO₂ saturation and nutrient limitation. Reproductive phenology of vegetation has been shown to respond to changes in temperature, particularly in temperate regions. While the temperature response in the tropics may be less apparent, shifts in rainfall seasonality could lead to disruptions in phenology, resulting in similar cascading effects on pollination, fruit production or other co-existence mechanisms (Cleland et al. 2007). This confirms the need to improve the dynamic vegetation models with more simulated processes and the usefulness of a dynamic vegetation model like

CARAIB relies on its ability to study whether a plant species is physiologically able to germinate and survive under future climate scenarios.

We cannot really predict the future. However, studying the outcomes of different models and scenarios can help us identify potential patterns or tendencies that can inform conservation practitioners or decision makers (Franklin et al. 2016). It seemed evident that not all species (irrespective of the taxa) are able to disperse enough, even if there are climatically appropriate zones identified in the future, outside their original distribution. Those whose dispersal is limited either due to natural or anthropogenic barriers, or other inherent behavioural, physical, or morphological traits are potentially at higher risk if they are unable to reach climatically appropriate areas (Root and Schneider 2006; Williams and Jackson 2007; Williams et al. 2008). Climate change impacts coupled with human-led habitat degradation may lead to higher risks for species (flora and fauna) compared to climate change impacts alone.

The 2009 global land-cover data shows a high level of fragmentation in the BAF region and in the GHLT range (Fig. 3.1 & Fig. 3.2), creating a mosaic landscape with different degrees of permeability for species (flora and fauna). Thus, a region that might still be climatically appropriate in the original distribution of a given species, may not necessarily permit germination, recruitment, and survival. In these regions, measures to mitigate potential climate change impacts, particularly for at-risk tree species may require direct reforestation, assisted regeneration, or protection efforts. While the GHLTs may not be at risk of complete extinction if a part of the tree species is lost (as in our MaxENT results), we can reasonably hypothesise that the quality and abundance of resources may impact GHLT survival in the long-term. This highlights the need for proactive conservation efforts to mitigate climate change impacts, as the loss in species distributions' is considerably lower in at least 3 GCMs for the more optimistic RCP4.5. Targeting a $< 1.5^{\circ}\text{C}$ increase in temperatures could imply potential to maintain some high level of diversity and functionality.

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Annex: Contrasting climate risks predicted by dynamic vegetation and ecological niche-based models applied to tree species in the Brazilian Atlantic Forest

Table 3.1. Annex. Input data requirements for MaxENT and CARAIB models:

	ENM	CARAIB
Distribution	Multiple species; lat-lon coordinates (does not model interactions)	Multiple species; lat-lon coordinates (will model competition for light and water)
Climate variables	Typically, BIOCLIM variables	Monthly meteorological variables from past to present (see detail below)
Other variables	Land-use (roads, urban areas, agriculture, topography, prey densities, etc.) – optional for habitat suitability modelling	Soil colour and texture; Plant traits (PFTs or species-specific); Fire management regimes (optional)

ENMs modelling can use raster files of environmental variables (climate data averaged like annual precipitation, mean temperature, humidity index or extreme values like minimum temperature of the coldest month – typically BIOCLIM variables; land-use – roads, urban areas, agriculture, topography; prey densities – often considered in habitat suitability analyses; etc. are some examples of environmental variables – depending on the nature of the question being asked) largely covering the known distributions of the species of interest. The samples of distribution are supplied as latitude-longitude coordinates, and multiple species can be simulated in one run but without interactions between the simulated species. Raster files of the same environmental variables are used for projecting into the future in the case of climate variable, the predicted changes in the future), or into a different geographical scope (in which case, the same resolution for a larger or different zone of interest), or both. The resolution of the models is the same as the resolution of raster of data.

CARAIB inputs include distribution samples as latitude-longitude coordinates for species of interest, and multiple species may be included which induces competition for light and water. The inputs include also a continuous record of a set of monthly meteorological variables from the recent past to the future (e.g. 1901 to 2100), over the study area from the selected GCMs. These variables are: mean air temperature, diurnal temperature amplitude, precipitation, wind speed, relative sunshine hours and air relative humidity. The soil colour and texture are also necessary. When possible, species-specific traits for specific leaf area, carbon-nitrogen ratios of leaves & wood, rooting depth, height, can be provided for each species; when these values are not available, the mean values of the plant functional types are used. The present-day climatic data allows to fix bioclimatic thresholds such as the lowest temperature supported by the species or the minimum requirement in growing degree-days above 5 °C. The climate of the early 20th century is repeated several times as a spin-up of the simulation, then the model is integrated transiently until 2100. There are options for land-use management and fire ignition-propagation to be simulated, if data are available/pertinent for the species and areas of interest. Typically, the model could be run on up to 60,000 cells, depending on the resolution of the available data inputs.

Table 3.2. Annex. Percent contribution of each bioclim variable. Estimates of relative contributions of the environmental variables to the Maxent model

Bio1 = Annual Mean Temperature

Bio2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))

Bio3 = Isothermality (Bio2/Bio7) (* 100)

Bio4 = Temperature Seasonality (standard deviation *100)

Bio5 = Max Temperature of Warmest Month

Bio6 = Min Temperature of Coldest Month

Bio7 = Temperature Annual Range (Bio5-Bio6)

Bio8 = Mean Temperature of Wettest Quarter

Bio9 = Mean Temperature of Driest Quarter

Bio10 = Mean Temperature of Warmest Quarter

Bio11 = Mean Temperature of Coldest Quarter

Bio12 = Annual Precipitation

Bio13 = Precipitation of Wettest Month

Bio14 = Precipitation of Driest Month

Bio15 = Precipitation Seasonality (Coefficient of Variation)

Bio16 = Precipitation of Wettest Quarter

Bio17 = Precipitation of Driest Quarter

Bio18 = Precipitation of Warmest Quarter

Bio19 = Precipitation of Coldest Quarter

MaxENT Species	Contribution of each bioclim variable																		
	bio1	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9
<i>Anacardium occidentale</i>	0.00	16.00	0.56	0.68	16.88	0.75	5.44	0.77	1.94	7.66	2.00	11.44	6.10	12.51	1.21	0.74	13.58	0.61	1.11
<i>Anomospermum reticulatum</i>	0.00	9.77	0.79	0.27	13.24	0.04	0.43	0.44	3.08	27.00	22.26	3.05	0.62	6.67	1.67	3.43	5.16	0.02	2.05
<i>Artocarpus heterophyllus</i>	0.50	0.00	0.00	0.00	0.00	10.97	0.31	7.86	3.72	5.23	3.15	5.65	0.00	17.57	5.57	12.01	8.42	19.05	0.00
<i>Bauhinia pulchella</i>	0.00	15.26	0.03	0.05	0.00	43.13	0.03	3.35	2.67	2.41	0.81	2.12	8.67	6.20	0.38	0.97	1.71	11.79	0.42
<i>Brosimum rubescens</i>	0.37	2.41	0.65	46.13	0.00	19.22	0.63	0.81	2.52	1.34	6.43	4.37	3.18	7.99	0.32	1.91	0.59	1.02	0.10
<i>Calyptranthes lucida</i>	0.00	0.00	0.00	0.00	4.23	0.20	0.92	0.00	1.11	0.00	75.10	0.00	0.00	13.54	0.00	0.00	0.00	4.90	0.00
<i>Campomanesia guaviroba</i>	11.77	8.83	0.00	0.00	1.53	0.07	0.01	0.00	0.36	16.04	0.66	10.27	10.09	24.05	6.02	9.08	0.05	0.02	1.17
<i>Caseiroa decandra</i>	1.20	8.65	2.19	8.22	4.27	23.37	2.66	0.33	10.25	0.18	10.57	1.55	5.08	6.99	2.44	8.92	0.71	1.78	0.65
<i>Cheiloclinium cognatum</i>	2.41	4.42	2.89	6.72	1.26	1.87	1.05	7.99	6.68	10.06	3.05	2.81	6.30	27.32	10.93	1.15	0.81	1.21	1.08
<i>Chrysophyllum splendens</i>	0.00	0.00	0.00	4.89	5.41	0.00	0.00	0.08	1.06	0.00	3.36	33.61	0.93	37.39	0.00	9.18	0.00	3.55	0.54
<i>Cordia bicolor</i>	1.58	6.10	4.81	0.00	11.33	0.18	5.66	3.51	3.54	5.47	2.63	4.73	3.96	15.81	0.30	0.09	18.12	1.90	10.28

	0.57	0.62	2.71	1.76	0.60	6.26	7.90	0.29	14.82	7.58	0.00	1.09	2.10	49.01	1.20	0.00	0.00	0.18	3.33
<i>Cordia ecalyculata</i>	2.89	0.83	8.01	0.29	1.14	19.59	3.59	7.61	25.79	0.27	7.61	1.81	1.54	8.75	2.91	0.02	5.80	0.75	0.81
<i>Diospyros hispida</i>	0.39	17.98	4.95	0.75	0.00	8.13	0.00	1.97	2.23	12.77	21.29	4.00	0.59	6.22	6.98	7.77	0.00	2.66	1.34
<i>Diplooon cuspidatum</i>	1.70	14.17	12.77	0.00	0.00	8.95	0.00	0.00	24.78	4.85	0.00	7.78	0.00	9.61	14.48	0.00	0.08	0.17	0.66
<i>Ecclinusa ramiflora</i>	0.02	12.19	0.03	0.10	1.22	5.23	0.36	0.00	20.86	22.20	17.06	1.60	0.37	13.88	0.00	0.09	0.04	0.00	4.75
<i>Eugenia involucrata</i>	0.88	14.63	47.67	0.38	0.00	0.75	2.56	0.00	0.14	0.35	0.10	0.00	0.08	30.58	1.86	0.00	0.02	0.00	0.00
<i>Ficus gomelleira</i>	1.43	3.07	5.10	0.00	0.00	0.29	3.01	4.57	9.59	0.39	36.14	1.26	16.70	16.43	0.00	0.50	0.00	0.34	1.18
<i>Garcinia macrophylla</i>	2.23	10.19	2.21	0.71	0.32	43.81	4.11	6.52	2.38	2.54	2.48	0.78	1.40	1.83	0.22	7.97	6.88	0.00	3.40
<i>Guapira opposita</i>	0.15	5.81	0.20	0.40	1.35	8.79	0.07	0.07	0.32	1.67	1.10	11.09	1.90	30.61	18.26	2.48	2.42	10.81	2.48
<i>Guettarda viburnoides</i>	0.00	13.00	0.58	23.29	1.27	4.27	1.45	2.12	3.75	6.88	0.95	6.22	16.46	4.46	0.49	5.64	0.42	7.52	1.22
<i>Helicostylis tomentosa</i>	4.65	3.05	10.87	1.25	0.28	6.32	0.48	11.76	20.52	9.13	4.60	4.15	5.00	11.47	2.74	0.25	2.25	0.69	0.57
<i>Henrietta succosa</i>	0.93	5.23	0.18	0.12	17.04	0.14	1.74	1.06	0.51	6.01	19.13	37.59	1.46	7.99	0.05	0.20	0.05	0.50	0.07
<i>Inga affinis</i>	1.42	1.84	0.00	0.00	0.06	10.58	0.47	0.00	17.40	1.52	0.28	3.70	0.90	45.13	5.28	0.00	0.00	3.70	7.72
<i>Inga edulis</i>	11.05	2.75	2.03	6.08	2.71	0.58	0.45	0.39	18.40	1.07	11.47	1.11	9.49	4.55	4.45	4.08	5.97	2.04	11.33
<i>Inga subnada</i>	16.02	0.64	2.76	0.01	0.30	2.24	0.91	0.73	0.03	0.00	0.83	36.16	4.49	10.48	13.93	9.78	0.00	0.69	0.00
<i>Licania discolor</i>	0.00	26.47	13.56	6.77	0.00	0.00	4.69	2.58	0.00	3.77	0.00	4.97	0.42	12.89	0.00	23.88	0.00	0.00	0.00
<i>Macoubea guianensis</i>	0.29	3.72	2.85	16.42	1.37	6.99	1.72	0.00	23.15	0.01	14.11	1.18	1.08	14.08	0.00	5.05	7.81	0.00	0.17
<i>Marlierea parviflora</i>	0.00	3.36	0.00	1.29	0.00	0.00	14.83	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	79.85	0.00	0.00	0.61
<i>Marlierea subacuminata</i>	0.00	0.00	0.00	0.00	0.00	0.00	1.04	0.00	0.00	15.70	19.06	6.25	47.73	4.61	0.32	0.00	0.16	0.00	5.12
<i>Miconia hypoleuca</i>	0.55	10.18	0.93	0.13	0.00	17.12	0.37	1.48	0.43	4.99	1.18	48.49	0.40	5.13	0.12	0.57	0.22	7.72	0.00
<i>Miconia mirabilis</i>	2.49	0.32	7.05	0.09	0.27	3.95	5.38	0.00	0.92	3.23	14.21	42.04	0.00	2.55	0.00	0.51	10.71	6.28	0.00
<i>Microphilia guyanensis</i>	3.00	3.00	5.76	12.58	1.07	5.12	11.29	2.36	19.31	5.66	0.92	1.06	1.46	23.21	0.05	0.89	1.08	1.10	1.08
<i>Microphilia venulosa</i>	3.92	3.58	1.96	29.31	1.46	3.64	2.53	5.94	13.20	7.31	1.29	2.91	1.19	16.28	0.85	0.91	1.45	0.40	1.87
<i>Musa paradisiaca</i>	0.24	5.43	26.70	2.65	0.04	1.37	1.69	0.92	0.00	1.76	8.72	3.00	1.87	15.80	8.26	4.28	14.53	2.44	0.30
<i>Myrcia fallax</i>	1.33	6.37	0.66	1.06	16.40	9.78	0.87	2.98	9.30	0.20	1.95	2.14	0.62	14.74	13.84	0.76	14.05	1.29	1.66
<i>Myrcia rostrata</i>	16.95	10.35	2.75	2.24	0.98	0.76	2.92	0.00	0.00	0.00	6.04	8.47	3.79	16.36	27.43	0.00	0.36	0.01	0.59
<i>Myrciaria floribunda</i>	0.04	3.65	5.26	0.56	12.46	1.36	3.55	4.03	6.66	4.06	2.96	15.94	8.51	9.52	11.29	0.67	1.16	3.36	4.96
<i>Neea verticillata</i>	0.00	7.21	0.94	0.32	0.00	68.79	2.32	0.09	0.80	0.24	7.55	0.00	0.00	1.78	0.10	0.00	9.66	0.00	0.20
<i>Orthomene schomburgkii</i>	0.08	1.50	0.41	1.18	11.01	1.62	15.99	0.25	15.61	1.70	1.83	4.38	0.15	15.29	5.16	8.69	10.22	1.88	3.06
<i>Posoqueria latifolia</i>	0.51	3.81	1.73	17.90	18.51	0.14	1.56	5.87	0.79	6.30	0.61	20.37	3.57	1.48	5.80	0.55	3.35	4.11	3.03
<i>Pourouma guianensis</i>	0.34	5.79	4.70	0.02	0.10	24.35	0.05	0.05	4.44	11.28	4.13	0.05	1.80	17.26	6.36	11.49	3.11	0.18	4.50

<i>Pourouma mollis</i>	9.98	10.99	0.46	0.68	0.08	44.01	1.02	0.00	0.10	0.13	2.20	0.83	3.48	22.78	0.12	0.10	1.22	0.99	0.81
<i>Pourouma velutina</i>	0.00	9.68	0.01	0.00	0.31	0.62	0.69	0.60	0.65	11.72	2.76	31.85	6.39	8.46	9.08	1.61	1.40	10.98	3.19
<i>Pouteria bangii</i>	0.54	24.06	5.22	0.08	0.01	25.09	1.47	5.08	3.58	2.98	0.04	0.01	0.56	16.24	0.01	14.20	0.30	0.53	0.00
<i>Protium aracouchini</i>	1.65	7.18	2.47	14.36	1.17	1.99	1.74	6.82	16.88	0.99	1.64	2.27	0.87	12.66	0.31	0.79	20.43	4.04	1.75
<i>Rheedia brasiliensis</i>	0.00	19.49	0.00	0.10	0.01	0.00	0.06	0.00	16.89	0.00	5.05	0.26	0.00	29.70	5.44	22.60	0.00	0.31	0.10
<i>Rheedia macrophylla</i>	2.46	17.42	4.59	0.20	4.25	3.57	1.53	0.00	26.65	2.00	26.68	0.00	4.00	5.75	0.00	0.83	0.00	0.00	0.07
<i>Rinorea guianensis</i>	0.04	52.16	1.72	0.32	0.00	34.80	0.00	0.00	0.14	0.00	0.86	0.02	0.00	5.87	0.00	0.00	3.98	0.09	0.00
<i>Sarcaulus brasiliensis</i>	1.54	1.96	0.58	0.95	1.34	20.30	1.92	0.00	19.17	30.85	0.02	1.60	4.43	6.77	1.36	1.83	5.19	0.05	0.14
<i>Simarouba amara</i>	1.09	1.53	10.10	10.70	4.55	1.37	5.02	1.42	1.01	5.78	6.63	8.82	10.41	9.89	0.44	11.97	7.19	1.54	0.54
<i>Sympmania globulifera</i>	1.57	1.16	6.30	36.96	0.28	0.65	0.53	5.12	2.21	13.44	5.85	6.67	2.84	7.56	6.69	0.96	0.57	0.36	0.26
<i>Tapirira guianensis</i>	6.19	2.49	4.33	20.71	1.22	6.02	1.41	0.86	21.20	4.73	0.86	3.43	8.72	11.35	0.72	1.90	3.16	0.33	0.37
<i>Terminalia dichotoma</i>	0.11	0.00	8.62	0.33	0.00	6.02	6.73	0.00	26.75	0.01	19.85	0.00	7.86	14.07	0.25	7.52	0.00	1.87	0.00
<i>Theobroma cacao</i>	2.40	2.99	4.60	2.62	0.82	0.33	2.53	14.27	13.28	1.34	3.69	20.23	5.04	6.35	4.32	8.41	4.34	0.33	2.10
<i>Thyrsodium spruceanum</i>	6.59	1.29	0.72	0.03	2.33	31.01	1.49	0.01	0.46	0.26	9.40	14.42	4.95	12.87	2.62	2.29	4.85	0.00	4.39
<i>Vismia latifolia</i>	2.67	1.66	2.72	0.34	15.35	0.14	2.61	0.02	3.42	2.81	9.81	38.76	6.99	0.21	0.00	9.56	0.02	0.04	2.88
<i>Xylopia sericea</i>	13.73	5.28	2.50	1.49	0.51	0.07	1.05	0.30	0.19	26.08	3.87	25.99	4.01	9.50	2.67	0.46	1.01	0.80	0.51
<i>Zanthoxylum rhoifolium</i>	19.23	2.67	4.99	0.88	6.16	0.96	1.29	4.97	1.40	11.47	6.62	3.83	1.06	13.84	2.72	0.40	5.50	3.55	8.47

Table 3.3. Annex. Agreement indicators: sensitivity, specificity, True Skill Statistic (TSS) and Area Under the ROC Curve (AUC) values for CARAIB (94 species) & MaxENT (59 species, missing values implies species not simulated in MaxENT)

Species	CARAIB				MaxENT			
	sensitivity	specificity	TSS	AUC	sensitivity	specificity	TSS	AUC
<i>Anacardium occidentale</i>	0.98246	0.12281	0.10526	0.60572	0.54688	0.89062	0.4375	0.83447
<i>Annona salzmannii</i>	1	0.17391	0.17391	0.54253				
<i>Anomospermum reticulatum</i>	0.91837	0.2449	0.16327	0.67576	0.70175	0.80702	0.50877	0.84518
<i>Artocarpus heterophyllus</i>	0.85	0.25	0.1	0.6325	0.66667	0.85714	0.52381	0.82426
<i>Bactris sedosa</i>	0.92857	0.35714	0.28571	0.66071				
<i>Bauhinia pulchella</i>	0.95775	0.21127	0.16901	0.50952	0.84848	0.80808	0.65657	0.91511
<i>Brosimum rubescens</i>	0.66071	0.55357	0.21429	0.63855	0.78571	0.85714	0.64286	0.89867
<i>Calyptrotes lucida</i>	0.92857	0.14286	0.07143	0.68878	0.76923	0.53846	0.30769	0.74852
<i>Campomanesia dichotoma</i>	0.4	0.6	0	0.52				
<i>Campomanesia espiritosantesnsis</i>	0.66667	1	0.66667	0.66667				
<i>Campomanesia guaviroba</i>	0.97561	0.09756	0.07317	0.68233	0.84906	0.81132	0.66038	0.90513
<i>Caseiroa decandra</i>	0.96262	0.15888	0.1215	0.64477	0.79699	0.90226	0.69925	0.88108
<i>Cecropia hololeuca</i>	0.86667	0.2	0.06667	0.57111				
<i>Cheiloclinium cognatum</i>	0.91241	0.29927	0.21168	0.71472	0.69192	0.86364	0.55556	0.88627
<i>Chondrodendron microphyllum</i>	0.875	0.625	0.5	0.92188				
<i>Chrysophyllum splendens</i>	0.85714	0.35714	0.21429	0.65561	0.80952	0.80952	0.61905	0.93878
<i>Cordia aberrans</i>	0.9	0.3	0.2	0.59				
<i>Cordia bicolor</i>	0.95082	0.2459	0.19672	0.69927	0.66197	0.92958	0.59155	0.92125
<i>Cordia ecalyculata</i>	0.75862	0.31034	0.06897	0.43163	0.92453	0.86792	0.79245	0.9717
<i>Cordia magnoliifolia</i>	0.78261	0.13043	-0.08696	0.53875				
<i>Cordia nodosa</i>	0.82427	0.37238	0.19665	0.66165	0.80299	0.85287	0.65586	0.90612
<i>Dialium guianense</i>	0.91176	0.48529	0.39706	0.75527				
<i>Diospyros hispida</i>	0.90909	0.29091	0.2	0.55934	0.83607	0.81967	0.65574	0.90876
<i>Diplopan cuspidatum</i>	0.88235	0.23529	0.11765	0.64187	0.89474	0.89474	0.78947	0.97784
<i>Ecclinusa ramiflora</i>	0.9	0.16667	0.06667	0.64278	0.75	0.85	0.6	0.88219
<i>Elaeis guineensis</i>	0.6	0	-0.4	0.4				
<i>Eugenia involucrata</i>	0.84	0.44	0.28	0.7784	0.81818	0.72727	0.54545	0.85847

<i>Eugenia robustovenosa</i>	0.6	0	-0.4	0.15				
<i>Faramea bracteata</i>	0.18182	0.72727	-0.09091	0.54959				
<i>Ficus gomelleira</i>	0.925	0.2	0.125	0.62031	0.7907	0.72093	0.51163	0.80882
<i>Garcinia macrophylla</i>	0.91935	0.25806	0.17742	0.7288	0.83	0.83	0.66	0.9187
<i>Guapira opposita</i>	0.9403	0.14925	0.08955	0.70483	0.87736	0.84906	0.72642	0.90517
<i>Guettarda viburnoides</i>	0.925	0.3	0.225	0.6142	0.85799	0.7929	0.65089	0.91611
<i>Helicostylis tomentosa</i>	0.91803	0.28689	0.20492	0.73267	0.8172	0.88172	0.69892	0.92391
<i>Henrietta succosa</i>	1	0.28571	0.28571	0.83418	0.70588	0.82353	0.52941	0.90484
<i>Hydrogaster trinervis</i>	0.5	0.66667	0.16667	0.68056				
<i>Inga affinis</i>	0.875	0.4375	0.3125	0.54883	0.92857	0.78571	0.71429	0.94452
<i>Inga edulis</i>	0.87582	0.24837	0.12418	0.62506	0.77376	0.8733	0.64706	0.91369
<i>Inga nutans</i>	0.7	0.6	0.3	0.6				
<i>Inga subnada</i>	0.82353	0.35294	0.17647	0.71972	0.80952	0.95238	0.7619	0.95805
<i>Licania discolour</i>	0.84615	0.69231	0.53846	0.68639	0.70588	0.70588	0.41176	0.80969
<i>Macoubea guianensis</i>	0.91429	0.45714	0.37143	0.77388	0.81132	0.84906	0.66038	0.92043
<i>Manilkara longifolia</i>	0.55556	0.22222	-0.22222	0.2963				
<i>Manilkara maxima</i>	0.66667	1	0.66667	0.94444				
<i>Manilkara salzmannii</i>	0.86957	0.52174	0.3913	0.8242				
<i>Marliera parviflora</i>	0.75	0	-0.25	0.25	0.8	0.6	0.4	0.76
<i>Marliera subacuminata</i>	0.6	1	0.6	0.88	0.8	1	0.8	1
<i>Marlierea regliana</i>	0.8	0.5	0.3	0.765				
<i>Mendoncia bahiensis</i>	1	0.5	0.5	0.75				
<i>Miconia cinnamomifolia</i>	0.875	0.20833	0.08333	0.60851				
<i>Miconia hypoleuca</i>	0.88571	0.14286	0.02857	0.63878	0.83333	0.85417	0.6875	0.95182
<i>Miconia latecrenata</i>	0.95652	0	-0.04348	0.63422				
<i>Miconia mirabilis</i>	1	0.06667	0.06667	0.73056	0.86842	0.78947	0.65789	0.9214
<i>Micropholis venulosa</i>	0.89116	0.22449	0.11565	0.6367	0.77982	0.87615	0.65596	0.91027
<i>Microphollis guyanensis</i>	0.86364	0.26136	0.125	0.67465	0.79508	0.86066	0.65574	0.91911
<i>Musa paradisiaca</i>	0.92308	0.23077	0.15385	0.69822	0.80556	0.80556	0.61111	0.89468
<i>Myrcia fallax</i>	0.92982	0.21637	0.1462	0.69654	0.8	0.87083	0.67083	0.89743
<i>Myrcia ilheosensis</i>	0.66667	0.83333	0.5	0.86111				

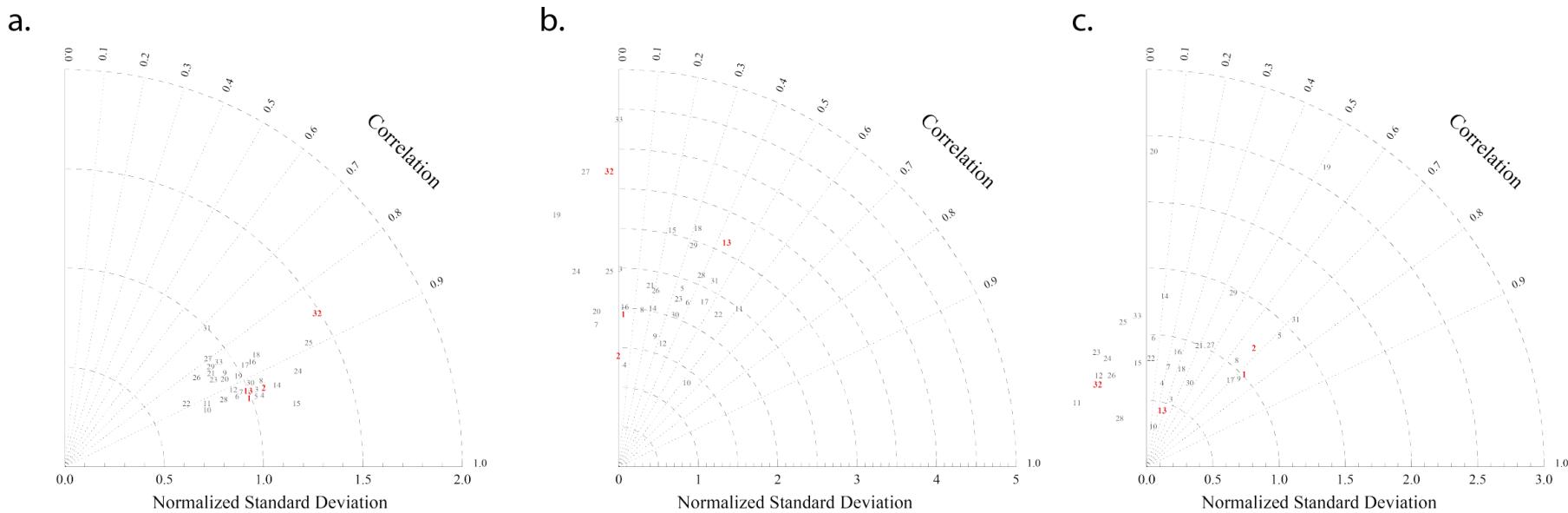
<i>Myrcia racemosa</i>	0.95238	0.19048	0.14286	0.73583				
<i>Myrcia rostrata</i>	0.85246	0.2459	0.09836	0.57847	0.8764	0.83146	0.70787	0.91844
<i>Myrciaria floribunda</i>	0.95556	0.19444	0.15	0.69435	0.72653	0.83265	0.55918	0.85932
<i>Neea verticillata</i>	0.38889	0.77778	0.16667	0.54012	0.93103	0.86207	0.7931	0.96195
<i>Neomitrannes obscura</i>	0.75	0.625	0.375	0.64844				
<i>Ocotea nitida</i>	0.7	0.26667	-0.03333	0.40222				
<i>Orthomene schomburgkii</i>	0.94565	0.15217	0.09783	0.65406	0.79675	0.85366	0.65041	0.9068
<i>Passiflora galbana</i>	0.92308	0.07692	0	0.69231				
<i>Philodendron williamsii</i>	1	0	0	0.48438				
<i>Posoqueria acutifolia</i>	0.76471	0.11765	-0.11765	0.57093				
<i>Posoqueria latifolia</i>	0.9589	0.20548	0.16438	0.7333	0.68333	0.87778	0.56111	0.87268
<i>Pourouma guianensis</i>	0.91045	0.1194	0.02985	0.62119	0.83505	0.90722	0.74227	0.91859
<i>Pourouma mollis</i>	0.88889	0.18519	0.07407	0.58985	0.79167	0.76389	0.55556	0.85928
<i>Pourouma velutina</i>	0.82759	0.31034	0.13793	0.66409	0.83333	0.94444	0.77778	0.9402
<i>Pouteria bangii</i>	0.63636	0.40909	0.04545	0.56818	0.7451	0.76471	0.5098	0.8564
<i>Pradosia lactescens</i>	0.83333	0.44444	0.27778	0.82407				
<i>Protium aracouchini</i>	0.91667	0.39286	0.30952	0.72307	0.78319	0.83186	0.61504	0.90567
<i>Protium warmingiana</i>	0.75	0.75	0.5	0.8125				
<i>Psidium cattleianum</i>	1	0	0	0.78				
<i>Rheedia brasiliensis</i>	0.78125	0.34375	0.125	0.54834	0.83721	0.88372	0.72093	0.93186
<i>Rheedia macrophylla</i>	0.83333	0.38889	0.22222	0.70563	0.73333	0.71111	0.44444	0.80568
<i>Rinorea guianensis</i>	0.9375	0.4375	0.375	0.65234	0.78947	0.73684	0.52632	0.87396
<i>Rollinia dolabirpetala</i>	0.95833	0.25	0.20833	0.67535				
<i>Sarcaulus brasiliensis</i>	0.85714	0.2619	0.11905	0.61593	0.79032	0.96774	0.75806	0.92963
<i>Simarouba amara</i>	0.90833	0.25833	0.16667	0.64455	0.68047	0.86982	0.5503	0.8722
<i>Solanum rupincola</i>	1	0.53846	0.53846	0.92308				
<i>Sorocea hilarii</i>	0.86207	0.13793	0	0.53092				
<i>Symphonia globulifera</i>	0.91971	0.30657	0.22628	0.70624	0.73077	0.91827	0.64904	0.91558
<i>Tapirira guianensis</i>	0.92926	0.28939	0.21865	0.717	0.73321	0.85605	0.58925	0.88517
<i>Terminalia dichotoma</i>	0.92308	0.61538	0.53846	0.81953	0.8	0.85714	0.65714	0.90735
<i>Theobroma cacao</i>	0.94505	0.16484	0.10989	0.62486	0.81203	0.84962	0.66165	0.90356

<i>Thrysodium spruceanum</i>	0.94872	0.15385	0.10256	0.67324	0.76923	0.76923	0.53846	0.85521
<i>Tibouchina elegans</i>	0.90909	0.36364	0.27273	0.77273				
<i>Vismia latifolia</i>	0.9375	0.46875	0.40625	0.76416	0.84906	0.90566	0.75472	0.96102
<i>Xylopia sericea</i>	0.92683	0.29268	0.21951	0.61243	0.71154	0.82692	0.53846	0.87999
<i>Zanthoxylum rhoifolium</i>	0.78571	0.23214	0.01786	0.55712	0.74658	0.84932	0.59589	0.89025

Table 3.4. Annex. Plant Functional Types (PFT) traits for CARAIB simulations, when species specific traits are not uniformly available.

Plant Functional Types	Specific Leaf Area Index (m ² /g C)	Root Depth (mm)	C/N leaves (mol mol ⁻¹)	C/N wood & roots (mol mol ⁻¹)	Height (m)
C3 herbs ("humid")	0.035	910	16	32	0.2
C3 herbs ("dry")	0.035	910	16	32	0.2
C4 herbs	0.035	1200	16	32	0.2
Broadleaved summergreen arctic shrubs	0.035	910	20	300	1
Broadleaved summergreen boreal/temp cold shrubs	0.035	910	20	350	1
Broadleaved summergreen temperate warm shrubs	0.035	1700	20	400	1
Broadleaved evergreen boreal/temp cold shrubs	0.035	910	25	400	1
Broadleaved evergreen temperate warm shrubs	0.035	1700	25	400	1
Broadleaved evergreen xeric shrubs	0.03	1700	25	400	1
Subdesertic shrubs	0.03	1700	25	400	1
Tropical shrubs	0.03	910	25	400	1
Needle-leaved evergreen boreal/temp cold trees	0.02	580	50	300	20
Needle-leaved evergreen temperate cool trees	0.02	1040	50	350	20
Needle-leaved evergr supra_mediterranean trees	0.02	1710	50	500	20
Needle-leaved evergr meso_mediterranean trees	0.02	1710	50	500	20
Needle-leaved evergreen subtropical trees	0.02	1040	50	500	20
Needle-leaved summergr boreal/temp cold trees	0.02	580	30	350	20
Needle-leaved summergr subtropical swamp trees	0.02	1040	30	400	20
Broadleaved evergr meso_mediterranean trees	0.03	1710	50	400	20
Broadleaved evergr thermo_mediterranean trees	0.03	1710	50	400	20
Broadleaved evergreen subtropical trees	0.03	1040	25	400	20
Broadleaved summergreen boreal/temp cold trees	0.03	580	20	300	20
Broadleaved summergreen temperate cool trees	0.03	1040	20	350	20
Broadleaved summergreen temperate warm trees	0.03	1210	20	400	20
Broadleaved raingreen tropical trees	0.03	1440	20	500	20
Broadleaved evergreen tropical trees	0.03	910	20	500	20

Figure 3.1. Annex. Examples of comparisons of GCM outputs to meteorological data in the form of Taylor diagrams to analyse spatial variability: (a) mean temperature, (b) mean temperature standard deviation, (c) mean temperature trend. The GCMs results are set in the plane according to their Pearson correlation coefficient with the observational data (short-dashed lines) and their normalized standard deviation (long-dashed lines). Perfect agreement between model output and observational data would bring a model on 1 on x-axis. In red, the GCMs selected for this study. Below, table of GCM rankings.



Ranking	GCM	Ranking	GCM	Ranking	GCM	Ranking	GCM	Ranking	GCM
1	HadGEM2_AO	8	HadCM3	15	CMCC_CM	22	MRI_CGCM3	29	GFDL_ESM2G
2	ACCESS1_0	9	IPSL_CM5A_LR	16	MPI_ESM_MR	23	GFDL_CM3	30	BCC_CSM1_1
3	HadGEM2_CC	10	FIO_ESM	17	IPSL_CM5A_MR	24	ACCESS1_3	31	GISS_E2_R
4	FGOALS_g2	11	BNU_ESM	18	MPI_ESM_LR	25	CanESM2	32	CSIRO_Mk3_6_0
5	HadGEM2_ES	12	CESM1_BGC	19	MIROC_ESM	26	IPSL_CM5B_LR	33	GFDL_ESM2M
6	CCSM4	13	CNRM_CM5	20	MIROC_ESM_CHEM	27	MIROC5		
7	FGOALS_s2	14	MIROC4h	21	NorESM1_M	28	INMCM4		

Figure 3.2. Annex. Examples of comparisons of GCM outputs to meteorological data in the form of Taylor diagrams to analyse spatial variability: (a) mean precipitation, (b) mean precipitation standard deviation, (c) mean precipitation trend. The GCMs results are set in the plane according to their Pearson correlation coefficient with the observational data (short-dashed lines) and their normalized standard deviation (long-dashed lines). Perfect agreement between model output and observational data would bring a model on 1 on x-axis. In red, the GCMs selected for this study.

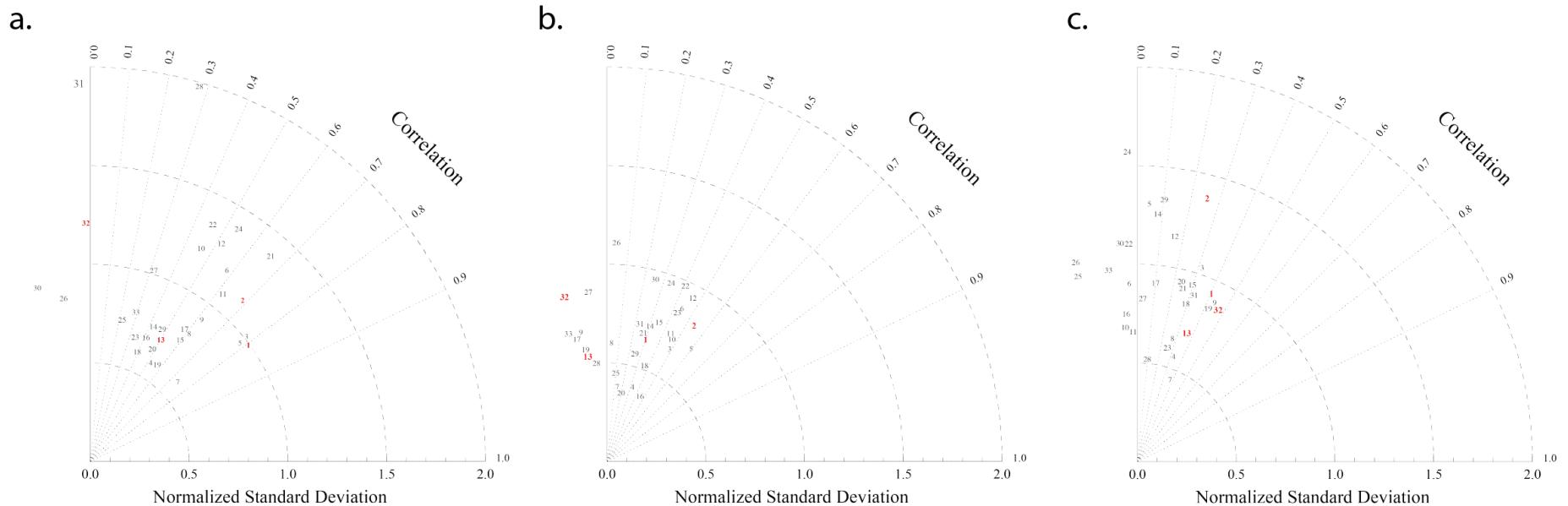


Figure 3.3. Annex. Annual mean temperature anomalies °C (a), annual precipitation anomalies mm/year (b), increase factor of soil water availability anomalies in relative units (SW-WP/ FC-WP; SW soil water, WP wilting point, FC field capacity) (c) between present-day simulation and RCP4.5 scenario for 4 GCMs

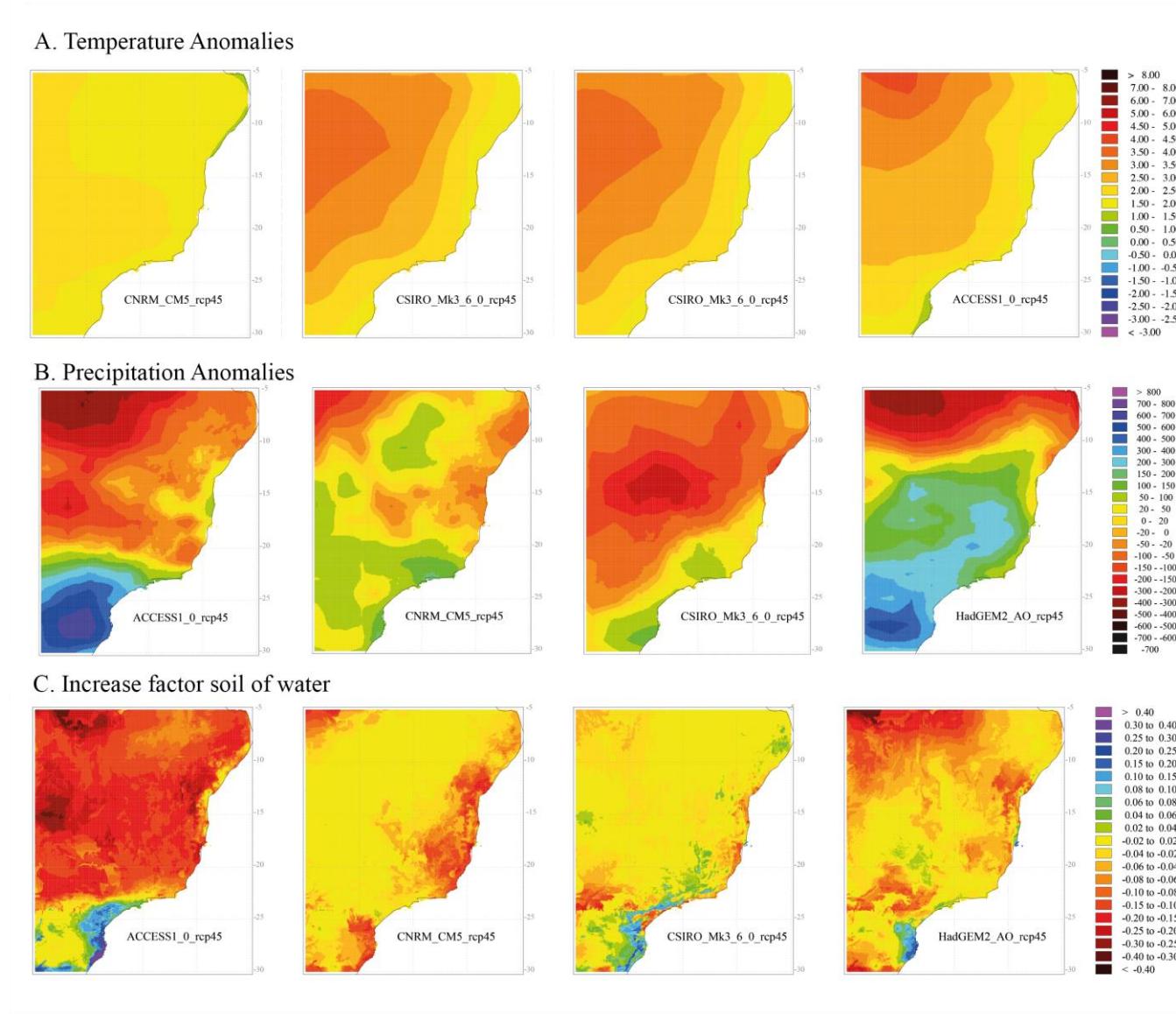


Figure 3.4. Annex. Comparison of changes in potential distributions between future and present-day simulations for 3 species between MaxENT & CARAIB in RCP4.5 ACCESS1_0 GCM simulated climate. Grey indicates areas where species was not predicted in the present-day nor future; light green areas are where the species was predicted in the present-day and in the future (i.e. grey + light green = no change); dark green areas are potential new sites to colonise (i.e. only distributed in future scenarios); red indicates areas where original predicted distribution is lost in the future. Yellow points are “current-day occurrences”

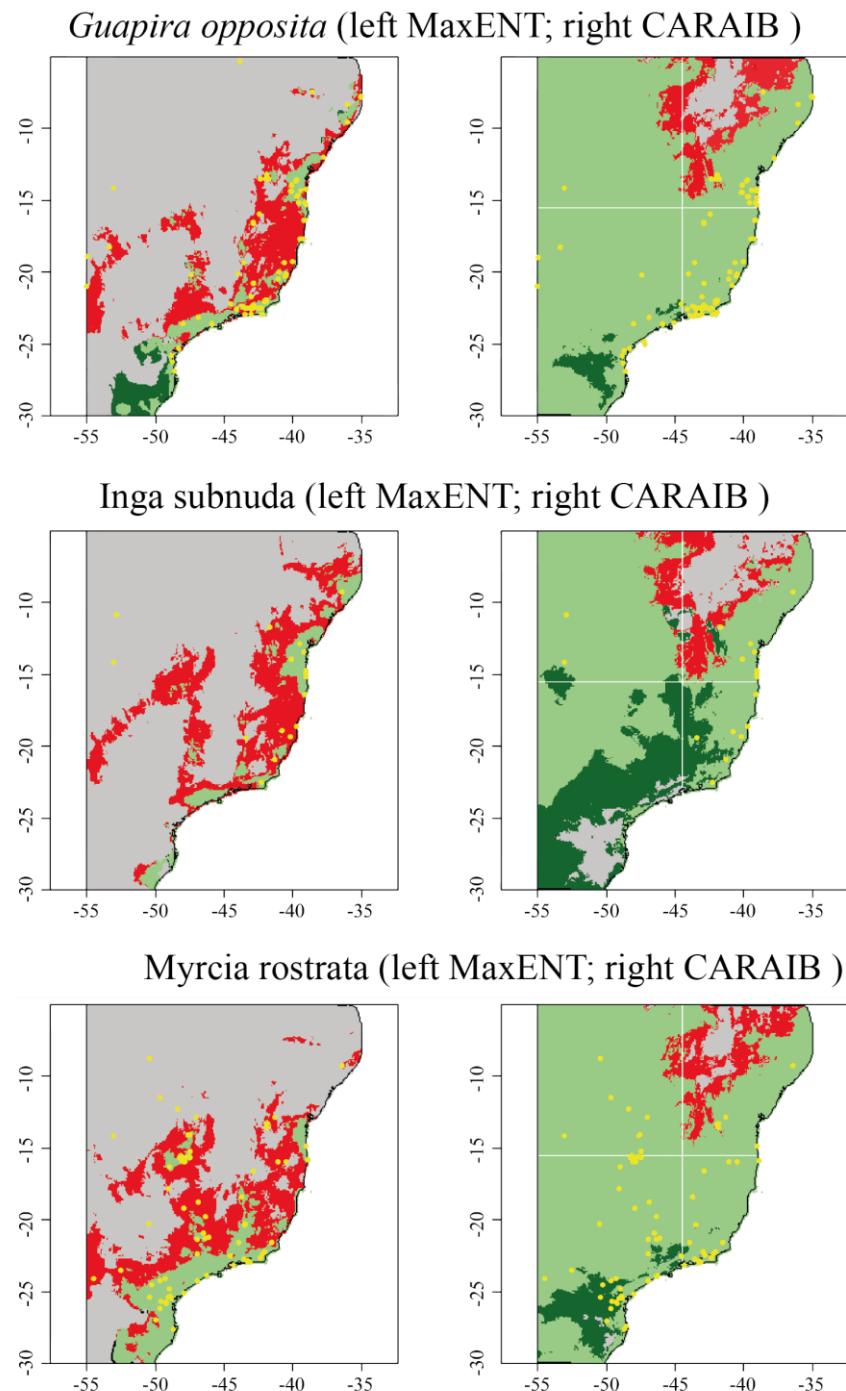


Figure 3.5. Annex. CARAIB without CO₂ fertilisation predicted distributions between present-day and future simulations in RCP8.5 and RCP4.5

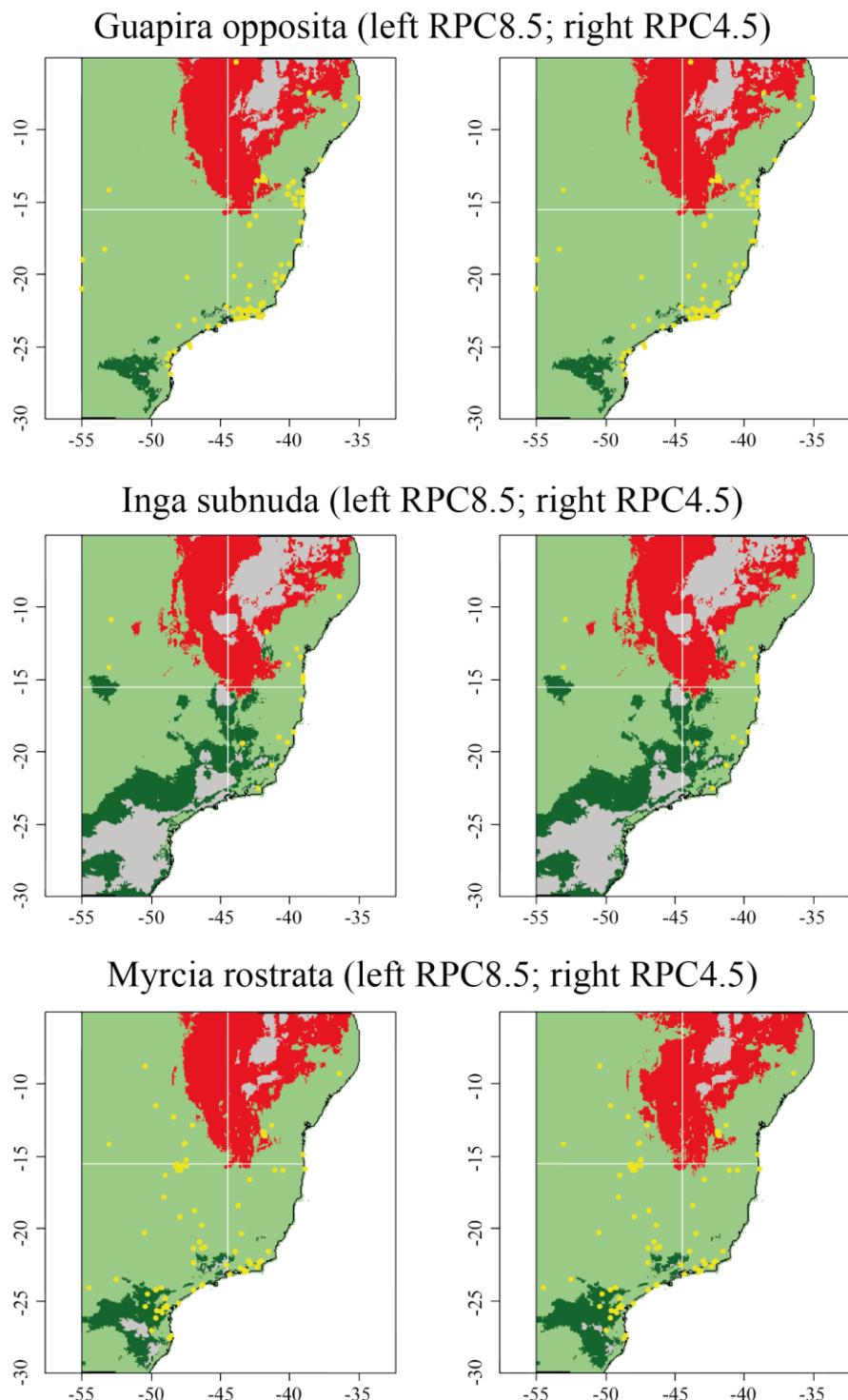


Figure 3.6. Annex. Percent loss of potential original distributions a. MaxENT, b. CARAIB, c. CARAIB without CO₂ fertilisation in RCP4.5 scenario

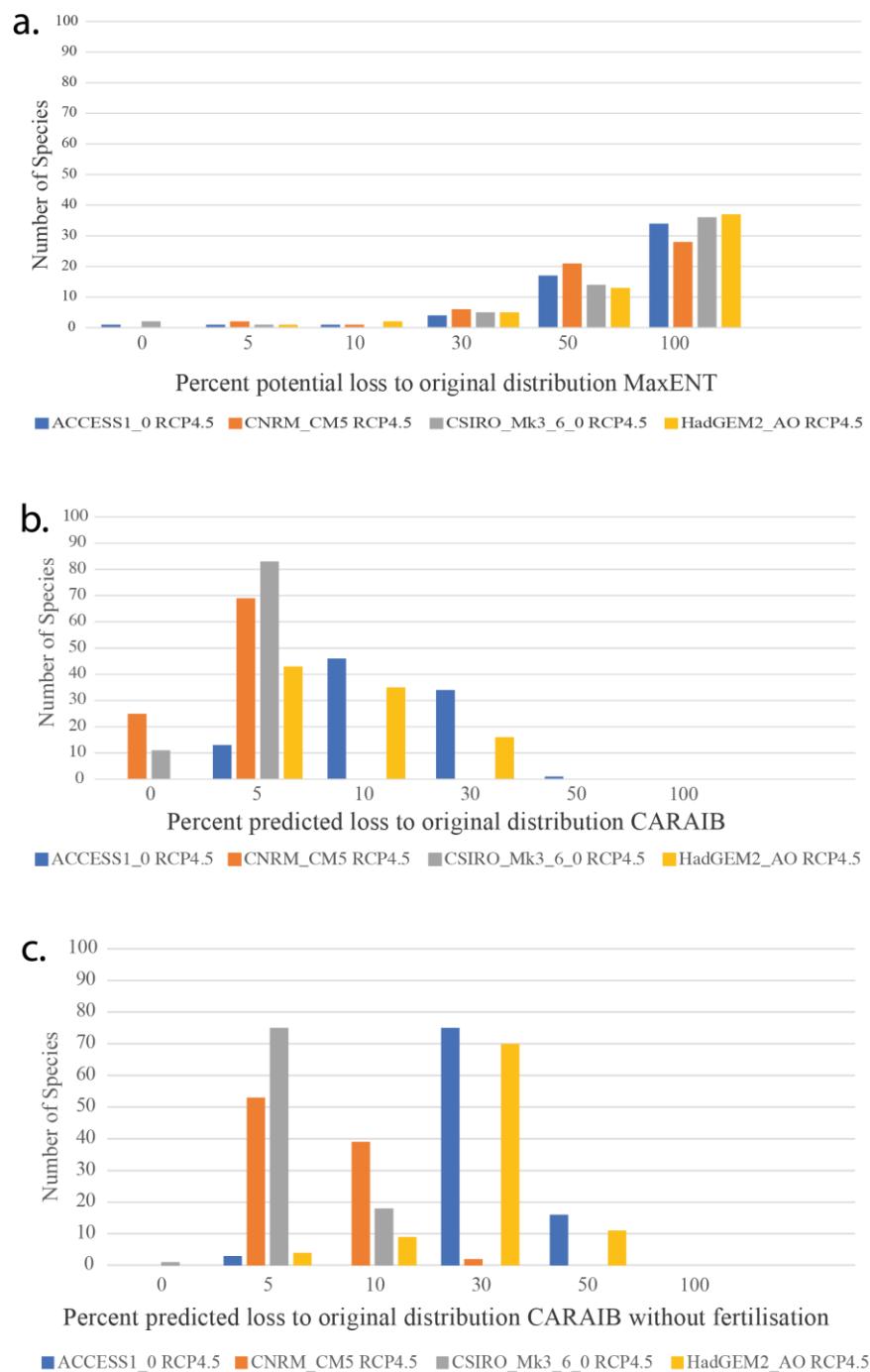
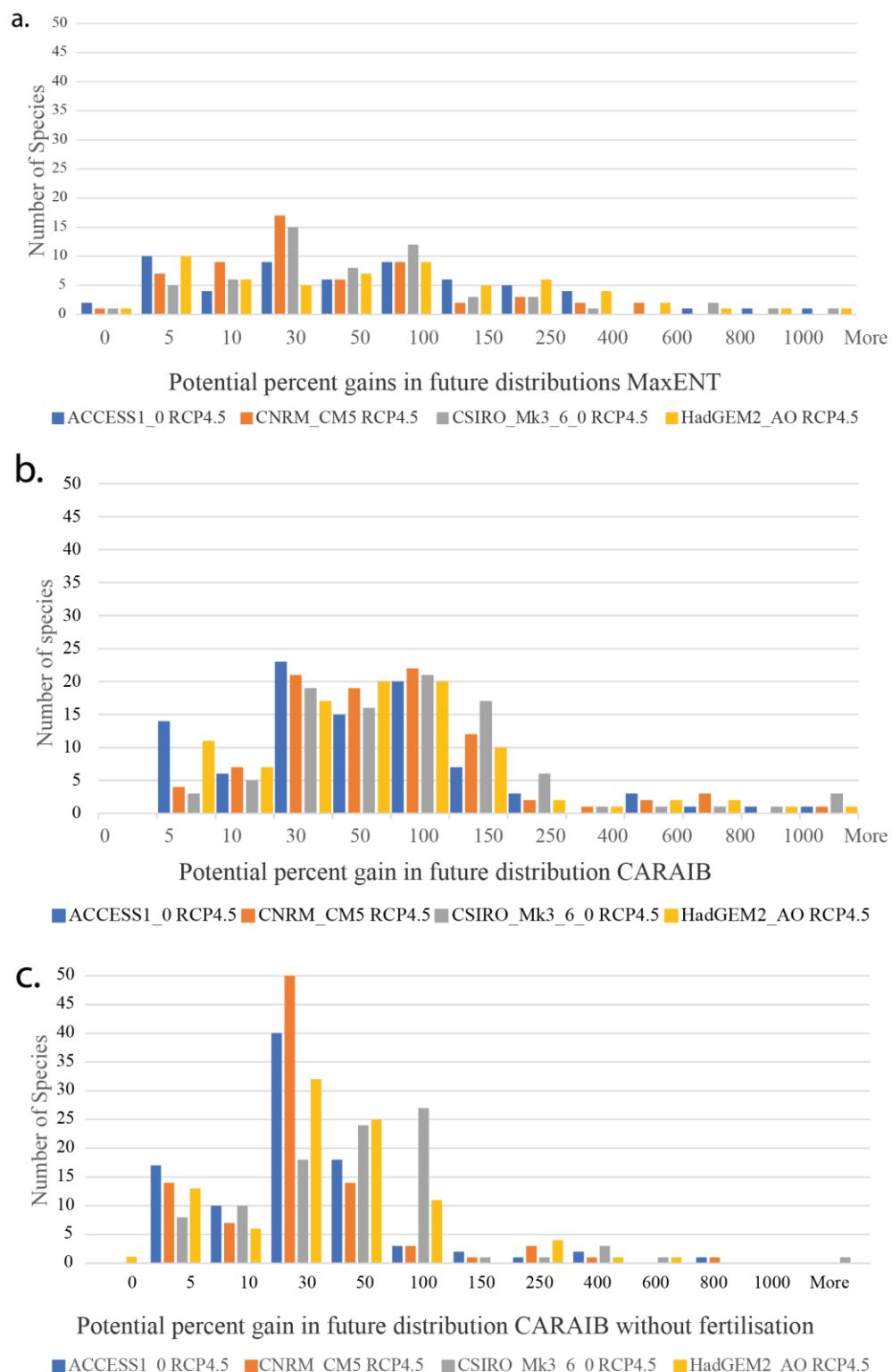


Figure 3.7. Annex. Percent gain in potential future distributions in a. MaxENT, b. CARAIB, c. CARAIB without CO₂ fertilisation in RCP4.5 scenario



4 Deterministic modelling of seed dispersal based on observed behaviours of an endemic primate in Brazil

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Abstract

In human-modified landscapes the likelihood of maintaining seed dispersal services mediated by animal's decreases, which in turn can threaten forest regeneration. With the objective of modelling their movement and their seed dispersal behaviour, we evaluated the role of a small-bodied, endangered, and endemic primate *Leontopithecus chrysomelas*, as a seed disperser, in the Brazilian Atlantic forest. To test their potential role in maintaining regeneration patterns in their home-range, through seed dispersal processes, we collected information on movement, seed swallowing and deposition, use of habitat, and characteristics of this habitat. We also analysed the daily trajectories using hidden Markov modelling. Our result suggests that the dispersal behaviour and short daily-trajectories of *L. chrysomelas* may play a small role in forest regeneration because it is only a short-range disperser. Nevertheless, *L. chrysomelas* probably contributes to increase the prevalence of its resource tree species locally, and thus likely to have a function in maintaining tree diversity by preventing local extinction. The collected information allowed us to build a deterministic Model of Seed Transfer (MOST) which was successfully able to replicate the primate's movement and seed deposition patterns, as observed in the field. This model combined with a dynamic vegetation model could be further used to test hypotheses of tree species survival by simulating tree regeneration and growth at regional scale.

Key words

Seed dispersal, frugivore, Atlantic forest, regeneration, Markov model

Introduction

We are facing the sixth mass extinction event (Barnosky et al. 2011). This current wave of species extinction could be attributed to a synergy among processes such as habitat loss, habitat modification, and climate change. The ability to reliably foresee how these threats could affect biodiversity in the future is of paramount importance for conservation planning. In theory, such information could be produced for terrestrial ecosystems with the help of Dynamic Vegetation Models (DVMs) allowing to spatially simulate plant distributions under different transitory environmental conditions (see for instance Raghunathan et al. 2015, 2018). DVMs could be coupled with agent-based models predicting land-use to take into consideration land use change (Fontaine et al. 2014). However, owing to inadequacy of dispersal data, specifically linking the relationship between plants and their dispersers, vegetation modelling suffers very often from low to no inclusion of plant dispersal and population dynamics. Accounting for seed deposition patterns is useful to predict the evolution of forest ecosystems (Reid et al. 2015). This task is particularly complex mainly in tropical forests, where a large proportion of trees (up to 90 %) have their seeds dispersed by animals (Howe and Smallwood 1982; Willson et al. 1989; Jordano 2000). Thus, vegetation modelling would benefit from combining information from frugivorous animal behaviour (movement, foraging, gut transit time of seeds) and DVM science.

Several studies have shown that the movement of animals (or groups of animals) within their home-ranges depends on the spatial distribution of resources like fruiting tree species, or more generally, their food resources, water bodies or sleeping sites (e.g. Albert et al. 2013a; Plante et al. 2014). Other factors, such as canopy cover limiting visibility to predators, connectivity, presence of liana conglomerates offering protection from rain and high temperatures, proximity to humans, and seasonality or weather conditions may also influence species' daily paths (e.g. Brotcorne et al. 2014; Granier et al. 2014; Neumann et al. 2015). For territorial species, potential conflict zones with other neighbouring individuals or groups can also influence their daily trajectories (Bateman et al. 2015). In the specific case for frugivorous animals, this dependency of the animals' movement on many environmental factors, coupled with the body size, will finally determine seed deposition within the environment (Holbrook 2011).

The seed dispersal process is affected by habitat loss and fragmentation, and ultimately climate change. As habitats shrink, it in turn causes disturbances in frugivore communities, for example, decreased abundance due to limited habitat availability, which carry over on plant communities, due to reduced dispersal. For example, Babweteera and Brown (2009) demonstrated that the loss of larger-bodied frugivores decreased the assemblages of larger-seeded, climax tree species in disturbed forest fragments. This was due in part to the specific dependency that larger seeded species

had on the presence of large-bodied frugivores, and because the small- & medium-bodied frugivores dispersed the seeds at smaller distances. The scale of fragmentation can affect how individuals or groups interact with distances to find habitat, and therefore alter their typical behavioural states (Cattarino et al. 2015). Animal species that may be highly territorial, or have emigrating individuals, that end up with a large density in a small patch of habitat may suffer from local extinctions if they are unable to broaden their home-range (Henle et al. 2004). Additionally, in fragmented or degraded landscapes that limit the animal movement, due to varying degrees of permeability within a mosaic, the seed dispersal services can be strongly altered both by loss of vegetation producing fruits (Pessoa et al. 2016) or change in fruits characteristics (Pessoa et al. 2017) but also due to behavioural constraints of frugivores (Trolliet et al. 2017a). Finally, climate change might alter availability of plant resources for the frugivores in the future (Raghunathan et al. 2015) and it might eventually directly challenge animal survival (Boyles et al. 2011).

It is well established that many frugivorous primates are efficient seed dispersers. Primates disperse seeds of several species, including hard-wooded species, in several habitat types like mature and secondary forests, or even savannahs and abandoned pastures (Chapman and Onderdonk 1998; Albert et al. 2013b; Bufalo et al. 2016; Trolliet et al. 2016). To build a deterministic model of seed dispersal based on observed data, we tested whether the endangered *Leontopithecus chrysomelas* (Golden-headed lion tamarins, GHLTs) in Brazilian Atlantic Forest (BAF) is an efficient seed disperser of the genus *Pourouma*. The choice of studying GHLT dispersal of *Pourouma* seeds was due to the fact that the seed size is one of the larger seeds that GHLTs are able to swallow (~11.9 mm by 10.5 mm), and the *Pourouma* species have a long fruiting season each year (typically from mid/end October to late April). Additionally, we were able to understand the potential role of GHLTs in forest regeneration in the study area. We first established the daily trajectory of a habituated group of GHLTs, and recorded fruit consumption and seed deposition events and other behaviours, in combination with environmental variables. Then, we analysed the movement in the home-range using a hidden Markov model (HMM) in relation to environmental variables. Finally, we conceived and coded, using FORTRAN, a deterministic model of seed deposition with random components by combining HMM, habitat characteristics and gastrointestinal transit time, which was able to simulate seed deposition. This model could further be coupled with a DVM and adapted to other animal and plant species.

Methods

Study sites

The 2015 study took place in Colônia de Una, Southern Bahia, Brazil (CU; 15° 17' 8" & 39° 8' 1"; SISBIO permit number 47178-1). The forest is classified as lowland Atlantic rainforest. The

region has an average annual precipitation of ~2000 mm/year, and average annual temperature at 24–25°C. The study site habitat is comprised mostly of regenerating areas, that were formerly rubber (*Hevea brasiliensis*), or rubber and cacao (*Theobroma cacao*) plantations. Some areas within the mosaic are still active for shade-grown cacao harvesting or banana production. De Vleeschouwer and Oliveira (2017) describe the characteristics of the rubber plantations in this area, suggesting potential reasons for the GHLTs to frequent such areas, despite anthropogenic activity that occurs within those parts of the habitat, the forested area is interspersed with some manioc plantations (*Manihot esculenta*), that are not used by the GHLT, and therefore not considered as part of their home-range. Position data were from the two other GHLT groups came from a 2006 study that took place in the Una Biological Reserve (UBR). Catenacci et al. (2009) describes the habitat in UBR, which is similar to CU habitat, however, with less anthropogenic activities, and a larger proportion of advanced secondary, largely due to its protected status.

Primate groups

All applicable institutional and/or national guidelines for the care and use of animals were followed. Data from three GHLT groups from two different studies were evaluated. At Colônia da Una, we studied one group of habituated monkeys. At the beginning of this study, the CU group comprised of 4 adults (2 males, 2 females), and at the end of the study, four adults, one juvenile, and one infant. With the two groups from the biological reserve, each group had 6 individuals (group 1: 4 adults, 1 juvenile, 1 sub-adult; group 2: 3 adults, 1 juvenile, 2 sub-adults). The habituation process was the same for the three groups and followed the protocol described in Dietz et al. (1996). At least one adult individual in each group had a radio collar affixed, to follow the groups using radio-telemetry. The groups were observed from sleeping site to sleeping site (i.e. from when they left the sleeping site in the morning, until the end of the day when they went into the same or different one). Every 20 minutes, we noted the coordinates using a Garmin etrex 30 GPS. Only complete observation days were used for analyses (26 days for CU group, 46 and 50 for the two UBR groups).

For the CU group, all behaviours relating to feeding, territoriality, predator presence, and resting/grooming, sleeping site use were recorded. Additionally, for the CU group, faecal samples were collected ad libitum. The *Pourouma* seeds obtained from faecal samples were positioned in different areas of the seasonal home-range, where the samples were collected, along with two control samples (with and without pulp) to test the effect of gut-passage on seed germination and survival. Locations of all scat deposits with *Pourouma* seeds were marked, and dispersal distances from parent-trees were estimated, based on average gut-transit time in GHLTs (Muñoz Lazo et al. 2011) and the visited trees before the defecation. Using ArcMAP v. 10.5.1. the seasonal home-range area was

calculated using the minimum convex polygon, though we also identified the 95% kernel – i.e. the zones with the probability of encountering the group is 0.95 (P95%).

Environmental data from Colônia de Una (CU)

To test for possible environmental variables that could influence GHLT movement in CU and later test the model, we installed seventy 15m by 15m plots located along transects spaced 30 m apart in the entire seasonal home-range of the group. In each plot we evaluated the basal area of fruit resources (BA), and the leaf area index (LAI). We estimated LAI by taking hemispherical pictures of the canopy. We took the pictures using Sigma 8mm f/4 circular Fisheye lens (Equi-angular projection) following the methods described in Bequet et al. (2012) at 9 points on the 15m by 15m plots; the pictures were analysed with Hemisfer v.2.16 (<http://www.schleppi.ch/hemisfer/>). In the plots, the trees were identified (at least to family level) for all individuals with a DBH > 5cm and the BA of the known fruit trees was calculated based on the DBH.

Additionally, within the seasonal home-range of the CU group, over a one-week period, we identified and mapped more than 600 *Pourouma* individuals and calculated the Fournier score (Fournier 1974) to obtain a snapshot of *Pourouma* fruit availability during the season. To obtain a Fournier score, the percent of fruit (ripe and unripe) available on the tree is scored on a scale of 0 (no fruit at all) and 1 to 4 (25% to 100%). Less than 25% of the *Pourouma* individuals have mature fruit at any given time during the fruiting season. The fruit availability index (FAI) was calculated by multiplying the Fournier score for presence of ripe or unripe fruit with the diameter at breast height (DBH) of all fruit trees that the GHLTs consumed. Finally, we interpolated FAI, BA and LAI over the entire seasonal home-range, using ordinary kriging in ArcMAP to obtain continuous maps.

Note that for the two other primate groups, no environmental data were available.

Effect of gut passage on seed germination and survival

The *Pourouma* genus control (with & without pulp; 80 seeds each) and treated (defecated; 85 seeds) seeds were distributed in 16 locations in the seasonal home-range, based on where scat samples were collected, in cages for protection. They were monitored each week, for the first 6 months of “planting”, to observe whether they had germinated, died (predation or parasite), or were missing (evidence of removal observed from small holes found where the seeds were placed, within cages). After 6 months, the 16 locations (245 seeds) were monitored monthly for a further 6 months, for a total of one-year of observation since “planting”. After one year, only the “recovered” seeds were analysed, in a mixed logistic model with the function 'glmer' of the lme4 R package (Bates et al. 2015) and the likelihood ratio test. The missing seeds were not considered in the analysis, so the sample size

of the “recovered” seeds included 14 seeds that germinated and survived as seedlings up to one year and 31 seeds that did not survive for the full year. The model included seed treatment (defecated seeds) and the two controls (with & without pulp) as a fixed effect, and the location within the seasonal home-range as a random effect of the intercept.

Movements in the home range

HMM requires positioning data at regular time slices. For each primate group, we prepared a single time series and trajectory, by joining end-to-end the coordinates of all the complete observation days. We applied the functions from the MoveHMM v1.2 R package (Michelot et al. 2016). In this analysis, the time series of positioning data are processed to obtain angle and step time series. These new series are used for the identification of changes in behaviour (step lengths, and turning angles) and the computation of probabilities of switching between states (Patterson et al. 2009; Langrock et al. 2012; Nabe-Nielsen et al. 2013; Pyke 2015). We used the gamma distribution for the step lengths and on the von Mises' distribution for the angles for which we easily found starting values by trial-and-error, by comparing the Akaike information criterion (AIC) of the possible models. Environmental variables (FAI, BA and LAI from the kriging maps) were tested as covariates, also with the AIC, for increased model fitness. The transitions between states are computed by the package with the equations provided in Michelot et al. (2016).

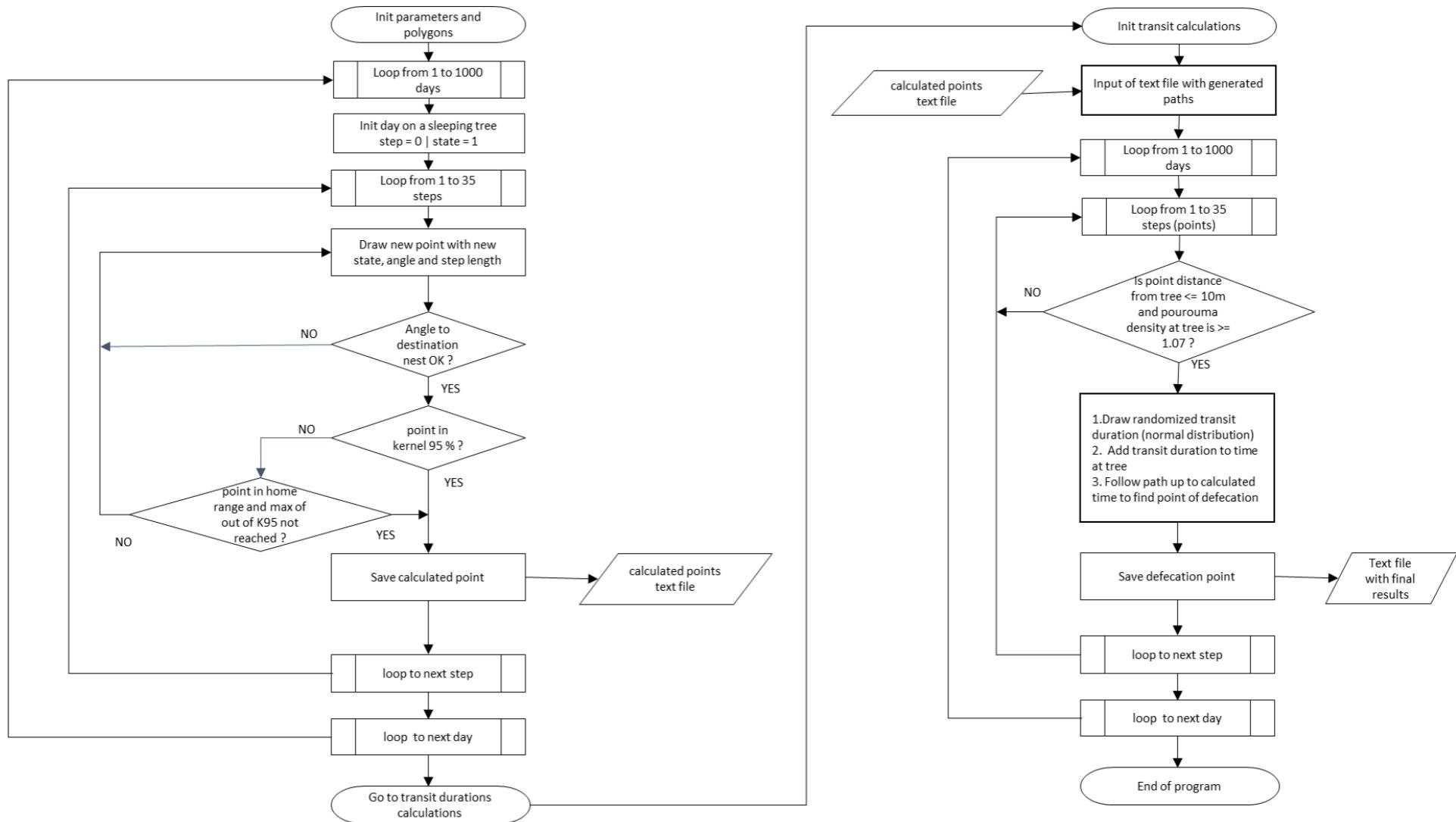
Deterministic Model of Seed Transfer (MOST)

The model (MOST for MOdel of Seed Transfer) was written in FORTRAN 90 to allow spatial extensions and further coupling with the CARAIB DVM also written in this language (Raghunathan et al. 2015). Most of the constants describing the home range, the movements and the animal behaviour and physiology, may be changed in a parameter file before program execution. While the GHLT groups do pass through tree covered areas, including the *seringa* and plantation zones, it is only used if there are important fruiting species, (*Artocarpus heterophyllus* in this particular zone, or bananas, etc.) or sleeping sites. In MOST, the plantation and agricultural zones were simplified to reflect “no-go” zones, though the monkeys may venture under the exceptional circumstances indicated above. In the case of the CU group, the principal sleeping site was also situated at the edge of a plantation area, and the trajectories reflect the short paths that traverse a small part of the no-go zone. The model (Fig. 4.1) starts by reading coordinates of home-range and kernel 95 % as well as sleeping site positions. A day path counts a succession of 35 steps (successive positions separated by 20 minutes), corresponding to an average day-length of 700 minutes, outside sleeping sites. The initial and the next selected nests were drawn from the re-use frequency. The simulation is initiated by setting the initial state of the HMM to one (note that we selected a two-state HMM) to know which of the distributions to use for angle and step. Accordingly, the first step and the first angle are drawn to reach the first position from

the starting sleeping site, using the gamma (step) and the Von Mise's (angle) distributions. As with first step, the procedure verifies that each position is located within the kernel 95 % using the "Winding Number" algorithm (Sunday 2001: [http://geomalgorithms.com/a03_inclusion.html#wn_PnPoly\(\)](http://geomalgorithms.com/a03_inclusion.html#wn_PnPoly())); if it is not within the kernel but still in the home range and maximum count out of kernel 95 is not reached (see below) then position is validated. Otherwise new angles and steps are redrawn until it becomes successful. The characteristics of the attained position are recorded and allow to draw the new state and accordingly to this state, the next angle and step to reach the next position. To simulate the end of the day, i.e. arbitrary after 26 steps, corresponding to the moment where the animals seemed to head to the sleeping-site, the drawn angles are progressively restricted from 360° to 22.5° to reach the selected sleeping site while the last step automatically drives on the selected nest position; possibly, they can arrive sooner when their position are less than 10 m. To be able to match the generated position frequencies within the P95%, we first analysed the density distribution of the number of positions of the observed trajectories outside the P95% using the fitdistrplus R package (Delignette-Muller and Dutang 2015). The obtained distribution with its parameters was used to generate a table of probable numbers of positions outside P95%. MOST records the trajectories, and stores for each of them its number of positions outside P95% and finally keeps only a subsample of trajectories providing the same numbers of positions outside P95% as in the table. *Pourouma* seed swallowing was provoked if the position was within a distance of 10 m of a *Pourouma* coordinates, and if pixel value of *Pourouma* mature fruit score was above 0.30. The distance has to be introduced as the likelihood that a given generated position will coincide directly with a fruit tree is highly infrequent. We examined the normality of the observed gut-transit time (Shapiro-Wilk normality test). For simulation, the procedure draws random values with corresponding distribution in the 95 % confidence interval of the mean of the observed values. The simulated spatial dispersal kernels could finally be calculated by recording the distances between the fruit trees and the defecation events.

For the validation of MOST's results, a chi-squared test for frequency was calculated, to evaluate the model's success at reproducing the observed distances of seeds in faeces from parent trees, as well as the distances to the closest conspecific.

Figure 4.1 Deterministic Model of Seed Transfer (MOST) algorithm used in Fortran programme.



Results

CU study site, group behaviour, and seasonal home-range

The seasonal home-range for the group in CU was approximately 18.77 ha, composed mostly of secondary forest in various stages of succession (Fig. 4.2). Six sleeping sites were observed in use with one sleeping site used more than 75 % of the times during the study, i.e. the group returned to the same sleeping site as they left in the morning 75 % of the times. The seasonal average of the daily path length for the group was 1,867 m, while the recorded positions outside the 95 % kernel could be considered as following a zero-inflated Poisson distribution (Fig. 4.3). During the *Pourouma* fruiting period, over the 26 complete observation days, we observed the group consuming fruits from 148 individuals and flowers from 21 individuals, from at least 30 identified species. Only four species had more than five visits (*Inga affinis*, *I. thibaudiana*, *Pourouma* spp, as well as *Artocarpus heterophyllus*), with one *Pourouma* fruiting tree having 26 visits during the observation period. Of the 169 foraged individuals, 73 were visited only once during the observation period.

Figure 4.2 Seasonal home-range of CU group. Coloured lines show some examples of daily trajectories of group (complete days) used for HMM analyses, blue areas show the 95% kernel within the seasonal home-range.

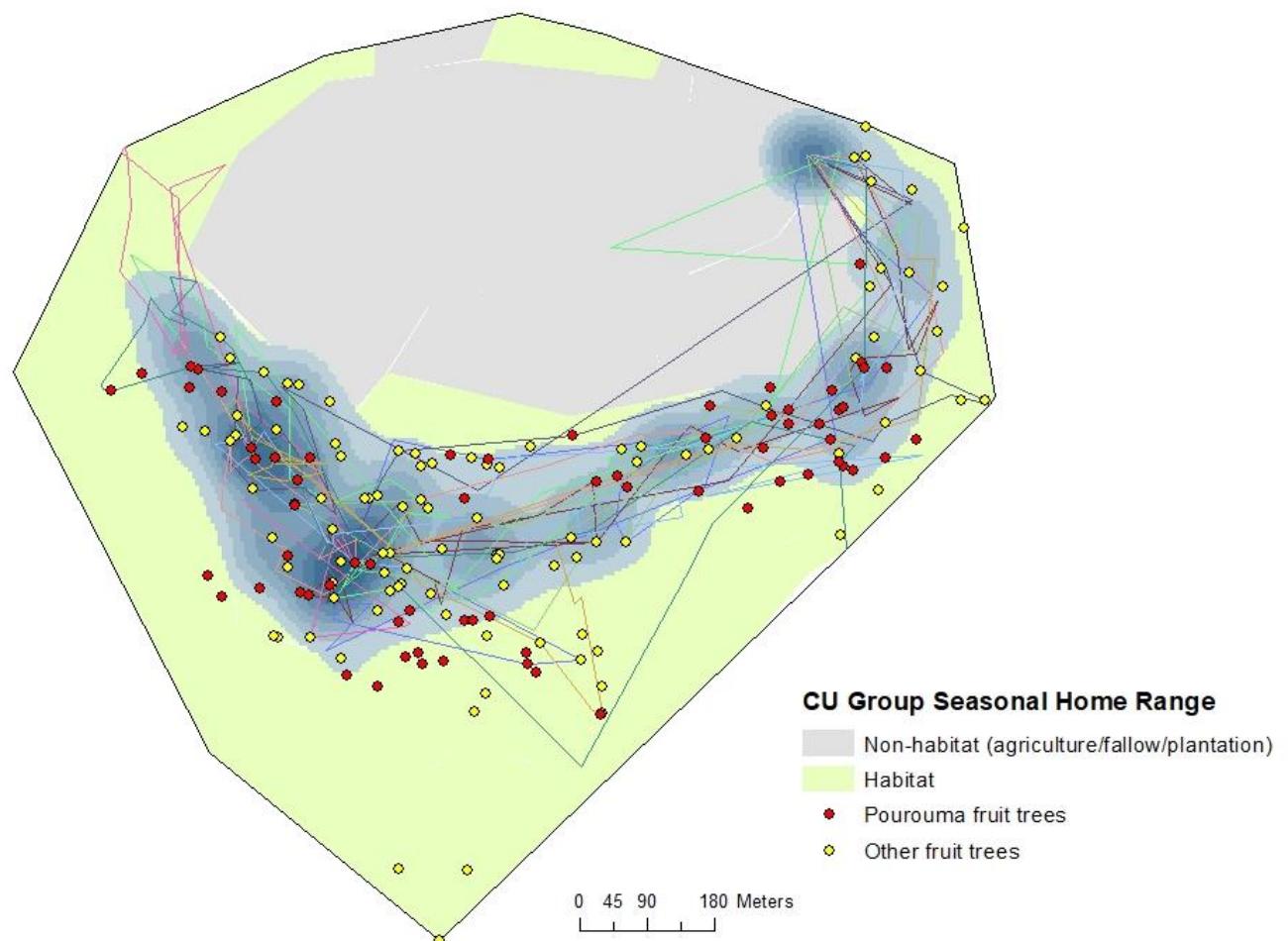


Figure 4.3 Density of positions outside of the 95% kernel (black) and adjusted zero-inflated Poisson distribution (red, $\mu = 4.27$, $\sigma = 0.298$, P-value of goodness-of-fit chi-squared test = 0.191)

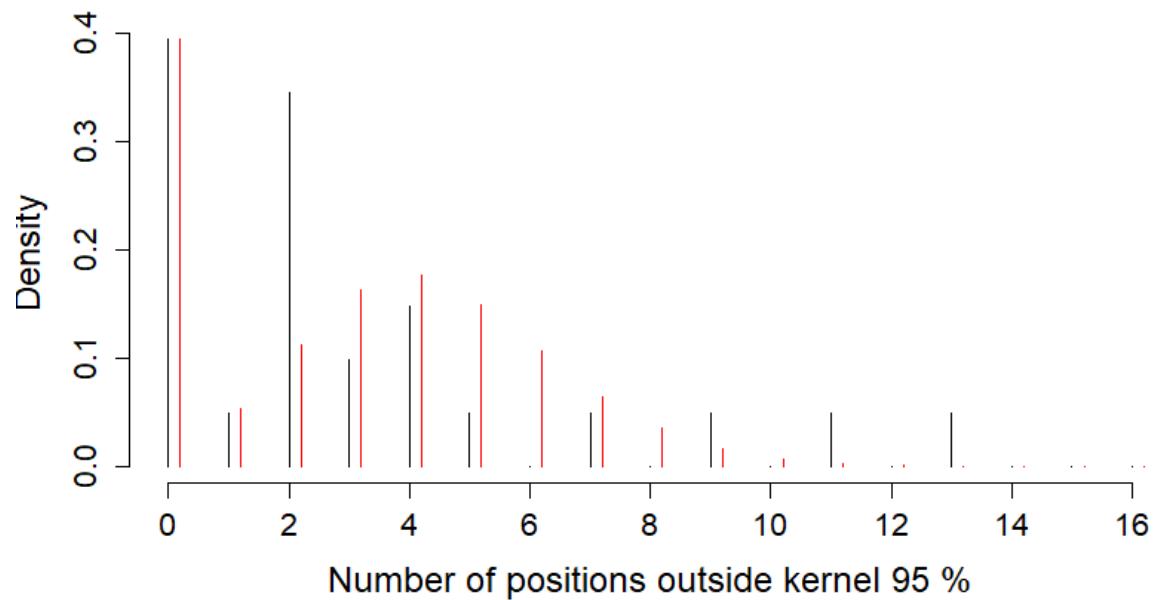
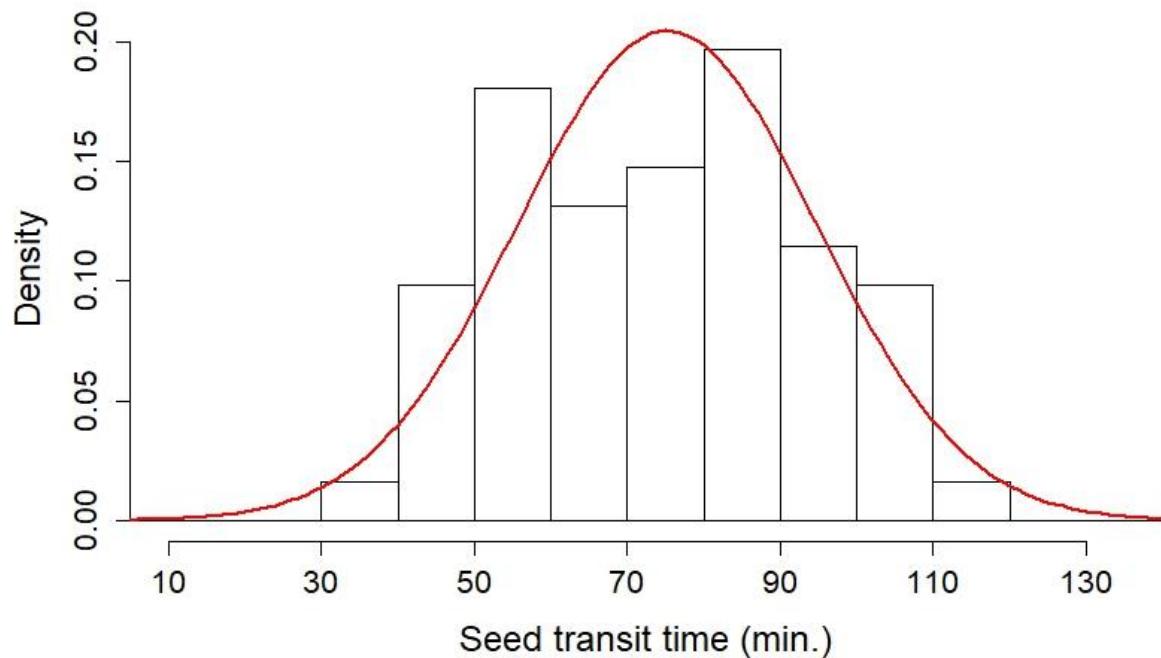


Figure 4.4 Observed (bars) and adjusted normal distribution of seed transit time (red line, mean = 75.20, standard deviation = 19.50, P-value of the goodness-of-fit Shapiro-Wilk test = 0.1432)



CU Environmental data

In the seventy plots, we recorded 2,216 trees, from more than 42 families. From those identified species, almost 50 % are species consumed by GHLTs, and the *Pourouma* genus represented 3% of the sampled individuals. LAI ranges between 0.088 and 2.005, BA between 0.08 and 0.26 m²/ha and *Pourouma* FAI Fournier score varied between 0 and 1.99 (see Annex for kriging maps of LAI, BA, and *Pourouma* density).

Faecal collection and germination data

Average gut transit times clearly follows a normal distribution (Fig. 4.4). During the *Pourouma* fruiting season, the CU group visited *Pourouma* trees daily. Average dispersal distances of *Pourouma* seeds was 111 m, with peak number of seeds deposited between 60 and 90 m (Fig. 4.5). Given the average transit time in the digestive tract and habitat use, most of the seeds were defecated near conspecifics. 80 % of all observed defecation events containing *Pourouma* seeds took place within 30 m of a conspecific, 20 % within 5 m of a conspecific tree (Fig. 4.6). Apparently, no significant effect of passage through the digestive tract could be observed compared to the two controls (chi-squared likelihood ratio test: =2.3579, degrees of freedom=2, p-value= 0.3076). Viable seeds may also have been defecated in highly unsuitable areas, when the GHLTs were foraging within bromeliads, or resting in liana conglomerates, with little possibility of germinating and surviving.

Figure 4.5 Observed (shaded) and simulated (blue) defecated seed distance densities from parent tree for CU group (chi-squared = 11.738, df = 6, p-value = 0.06807)

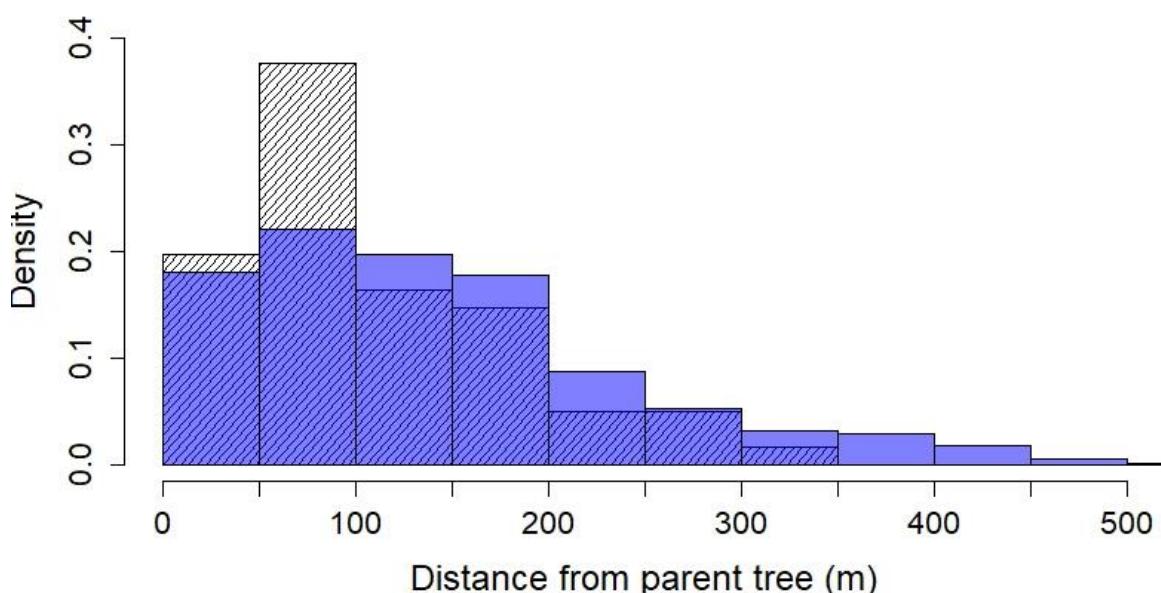
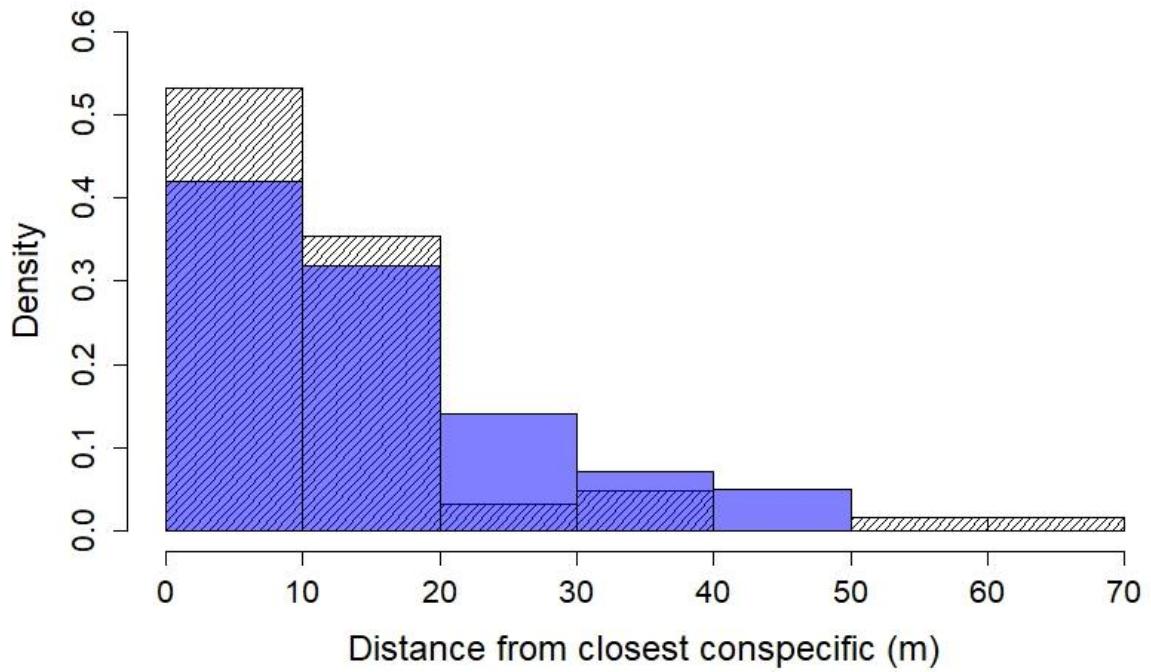


Figure 4.6 Observed (shaded) and simulated (blue) defecated seed distance densities from closest *Pourouma* conspecific for CU group (chi-squared = 78.1645, df = 4, p-value = 0.08573)



Hidden Markov model

For the CU group, we selected a two-state HMM, with basal area of fruiting species, along with distance from sleeping sites being key predictors of transition (Table 4.1), based on the AIC. State 1 comprised the longest step lengths, shorter turning angles, and fewer pauses, while state two was characterised by shorter step lengths, larger angles, and more pauses. For the two other groups (UBR1 & UBR2), we were able to select only one-state HMM, based on the XY data (Fig. 4.7).

Table 4.1 Selection of the hidden Markov model (HMM) simulating animal movements within the home-range. AIC values with combinations of the environmental variables (basal area of fruiting trees: BA, distance to sleeping site: SS, fruit availability index: FAI, distance to bromeliads: BRO, distance to fruiting trees: FT, leaf area index: LAI, distance to predator: DP, distance to other group: DG, distance to resting sites: DR) and parameters from best-fit model subsequently used in MOST.

Model	AIC
BA+SS	620.14
BA+FAI	622.76
BA	638.96
DS	649.33
Null Hypothesis	662.05
BRO	662.26
FAI	662.63
DG	664.20
DR	664.21
FT	665.52
DP	668.87
FAI+SS	806.50
BA+FAI+SS	810.80
LAI	828.43

Selected model: BA+SS

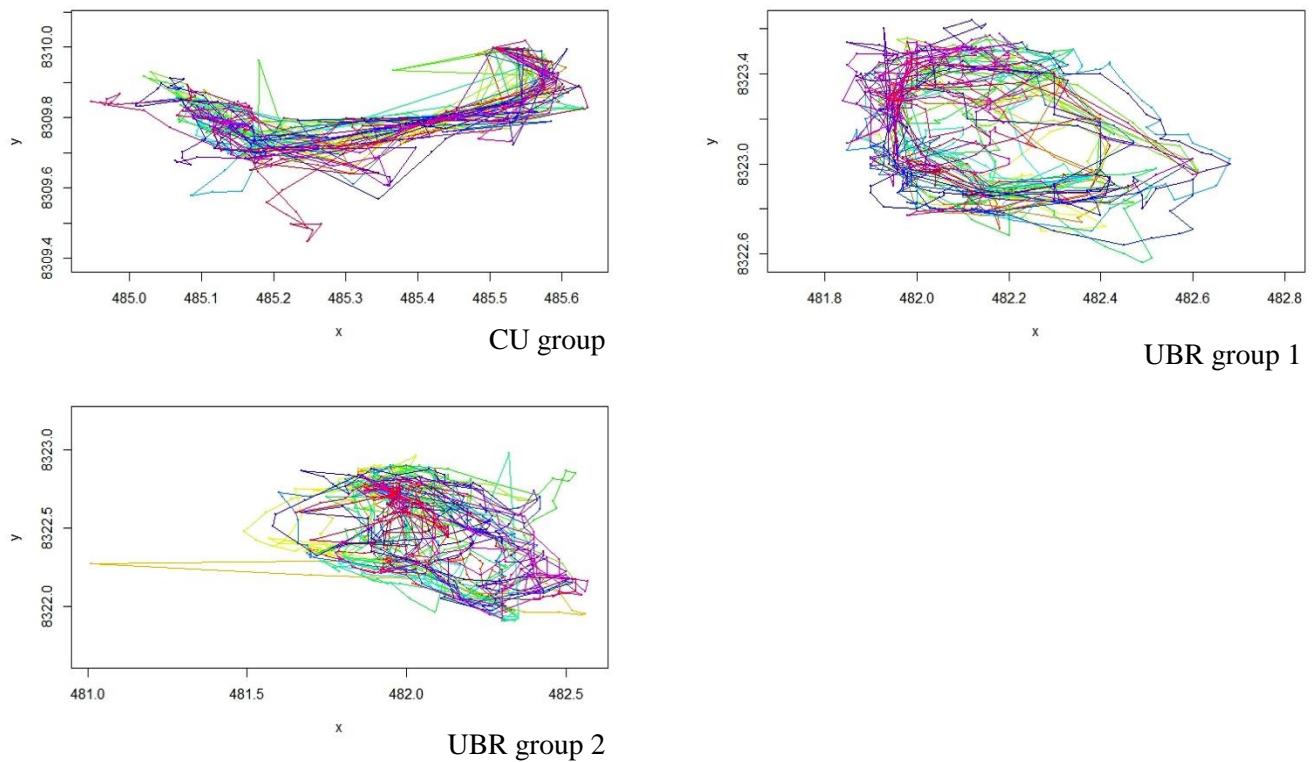
Value of the maximum log-likelihood: -293.0703

Gamma distribution parameters (step length)		
	state 1	state 2
mean	0.102	0.036
sd	0.058	0.026
zero-mass	0.026	0.154

Von Mises' distribution parameters (turning angle)		
	state 1	state 2
mean	-0.018	0.026
concentration	0.990	0.415

Regression coefficients for the transition probabilities		
	1 → 2	2 → 1
intercept	-2.539	-1.023e+01
SS	0.005	5.315e-04
BA	1.392	5.711e+01

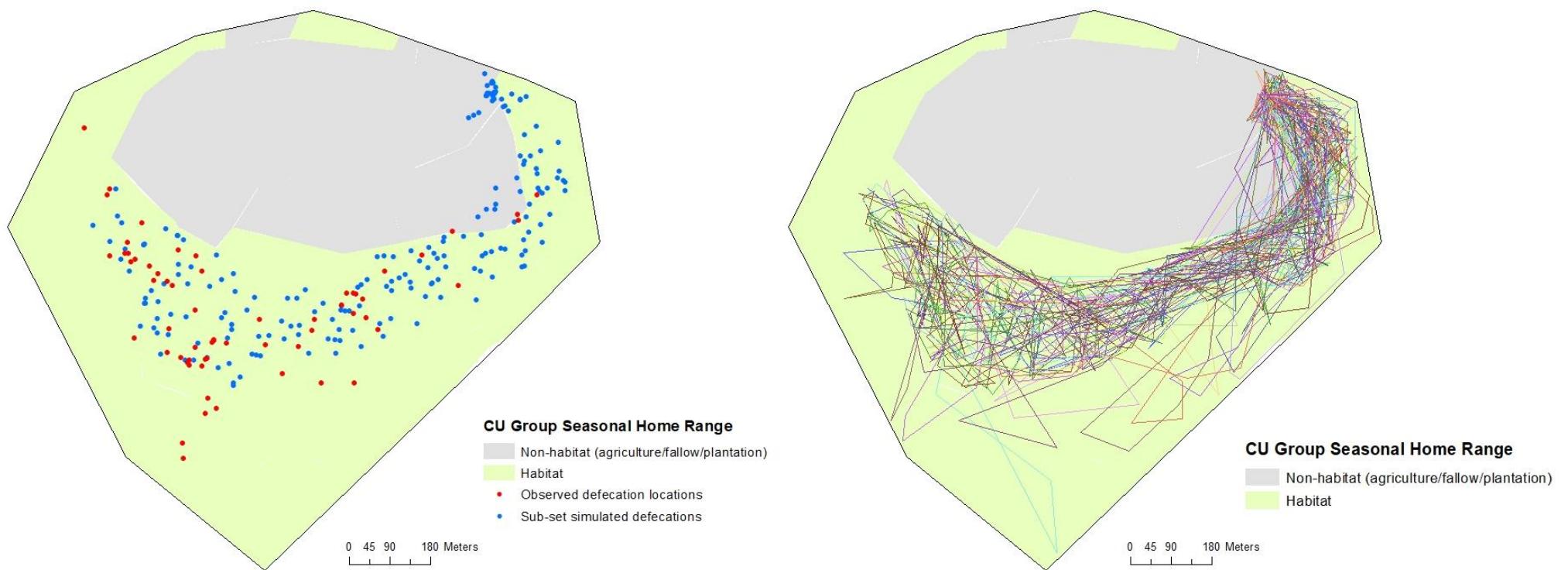
Figure 4.7 Trajectories of 3 groups (CU seasonal trajectories, 26 days; UBR group 1 – annual trajectories, 46 days; UBR group 2 – annual trajectories, 50 days), UTM coordinates on axes



Deterministic Model of Seed Transfer (MOST)

MOST was able to successfully simulate two-state trajectories within the CU group's seasonal home-range (Fig. 4.8) but the simulations were sensitive to the threshold value for mature fruit and the distance to *Pourouma* to provoke swallowing and the final values were obtained through some trials & errors (distance of 10 m and *Pourouma* FAI of 0.3, see also Annex). The simulated distances of seed deposition were not significantly different from those observed (Figs. 4.5 and 4.6) but this could be improved by finer selection of distance and FAI threshold. Distance from parent tree showed longer tail as expected, since more events than observed were simulated and tended to reveal more extreme values but it did not appear in distance from closest conspecific.

Figure 4.8 Map of sub-set of simulated defecation events, with distance to *Pourouma* of 10 m and mature fruit threshold of 0.3, from MOST and observed defecation events within the seasonal HR of GHLTs (left) and sub-set of simulated trajectories (right).



Discussion

Using HMM analyses we were able to identify main factors influencing GHLT movement, which in turn affects the seed shadows and regeneration processes. The daily trajectories of the GHLT group, and the local factors influencing them are concordant with the literature on variables affecting animal movements: food resource and sleeping site distribution (e.g. Palminteri et al. 2012; Albert et al. 2013a). Considering the small seasonal home-range size, coupled with a relatively high abundance of potential food sources, the effect of fruit availability on movement may be diluted; futures studies could be refined with phenological data. Parameters used to initialise HMM analyses therefore are influenced by habitat composition and home-range size. As the choice between the states (2 or more) relies on thorough biological knowledge of the group or individuals of interest, the parameters appropriate for one group may not be relevant for others, as evidenced by the differences between the CU and UBR groups. The HMM two-state model parameters are directly linked to the home-range characteristics of the groups, therefore for each application of the MOST model, environmental characteristics of the home-range characteristics must be supplied to test dispersal behaviours.

Studies of GHLTs within more continuous forested areas (Una Biological Reserve - Cardoso et al. 2011) showed that GHLTs do in fact play a role as dispersers, by consuming fruits and swallowing seeds in the mature forest and defecating seeds in secondary, or agro-forestry systems within their home-range. However in more degraded habitats, a similar pattern as observed in the CU group was observed, with the GHLTs contributing to dispersal of smaller seeds of pioneer species and bromeliads (Catenacci et al. 2009), and less to medium or larger sized seeds of fruits, that form an important part of their diet. Our results suggest that within a degraded, mosaic habitat, GHLTs may maintain their habitat at a local level or eventually improve the availability of its resource species, but only inside its 95% kernel seasonal home-ranges. This should not be disregarded because it is probably a mechanism fostering species local abundance and preventing local extinction. The small-bodied GHLTs does not allow them to functionally replace other larger frugivorous taxa that may be locally extinct, and we cannot anticipate whether the dispersal services currently performed by the species would maintain the existing diversity in the long-term, particularly in their small seasonal home-range. The evidence regarding dispersal distances from parent-trees and conspecifics is unclear, with some studies (Webb and Willson 1985; Hubbell et al. 2001; Forget et al. 2005) suggesting that seeds deposited even a few meters away from the parent's canopy will be more likely to germinate and survive, and others (Howe 2016) suggesting that depositions closer to conspecifics can decrease germination success. While it is suggested that zoolochic maximal dispersal distance could be related to home-range size (Pakeman 2001), this could give a false image of the real dispersal efficiency since it does not take into account the dispersal away from the conspecifics. The enrichment of plant

diversity within the GHLTs habitat may rely on birds and bats that were routinely observed during field work, or on other species like *Callithrix kuhlii* (Wied's marmoset), or *Potos flavus* (kinkajou), which we also observed in the field and also reported in the eastern Atlantic Forest (Helgen et al. 2016). Considering the spatial distribution of seed deposition, we can conclude that the efficiency of each disperser of *Pourouma* is not redundant, because each dispersing species travels in its habitat following particular behaviours. For instance, bats are considered good dispersers because they can travel several kilometres each day, and defecate when flying (Oleksy et al. 2017) but they generally show high fidelity to swarming sites (Glover and Altringham 2008; Bologna et al. 2018; Gonsalves and Law 2018) which should produce highly directional dispersal kernel. Finally, the low ability for seed dispersal of GHLT could be viewed as a cascading effect of fragmentation on loss of ecosystem services since fragmentation restricts GHLT in possibly smaller forest fragments.

The dispersal module built to simulate dispersal could be used to evaluate the rate at which a given tree species might colonise new sites, based on the behaviour that are included as parameters. The CU group's dispersal distances are consistent with other studies on *Leontopithecus* genus and *Saguinus* species (Cardoso et al. 2011). However, it is important to keep in mind that in the case of generalist frugivores, smaller home-range areas with a uniform distribution of fruit resources might dilute any potential patterns or states in behaviour. This appears to be consistent with Nabe-Nielsen et al. (2013), where they suggest movement states can change based on temporal scales and heterogeneous nature of the home-range. Therefore, the parameters for displacement will need to be determined for each group whose dispersal is to be simulated.

Conclusion

As habitat modification and loss become an increasing threat to tropical fauna, measures must be taken to ensure viability of ecosystem functioning in the long-term. While designating protected areas is one strategy, the success of which depends on the management and enforcement of sustainable-use plans, other strategies to improve connectivity between forest patches, or restore areas through assisted regeneration can become important. Studies suggest that with careful management, the natural dispersal behaviour of frugivores within the tropics could in fact accelerate the restoration and functionality of degraded habitats. In this context, understanding frugivore movement in relationship with resource species becomes exceedingly critical, to be able to protect and to ensure maintenance of dispersal activities. The analysis of GHLT behaviour demonstrated that it is a short-range disperser because most seed deposition occurs near conspecifics, but it is probably a particular case, with a smaller than average home-range mostly relying on highly clustered *Pourouma* trees. The fact however that simulations were able to generate 'true-life' defecation patterns show that the dispersal module MOST combined with a DVM can be a useful tool to test hypotheses of tree species

survival by simulating tree regeneration and growth at regional scale, providing the inclusion of behavioural, physiological and abundance data for as many as possible dispersal agents of the area of interest and land use. An alternative approach would be to use the model combination to perform experiments using only available information, by varying the numbers and the types of dispersers, as well as land configuration to test the existence of thresholds preventing the extinction of selected tree species.

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Annex: Deterministic modelling of seed dispersal based on observed behaviours of an endemic primate in Brazil

Figure 4.1. Annex. Distribution of GHLTs in Brazil (endemic to Southern Bahia and Northern Minas Gerais)



Figure 4.2. Annex. Kriging interpolation of *Pouroma* individuals using Fournier score for density on fruit availability.

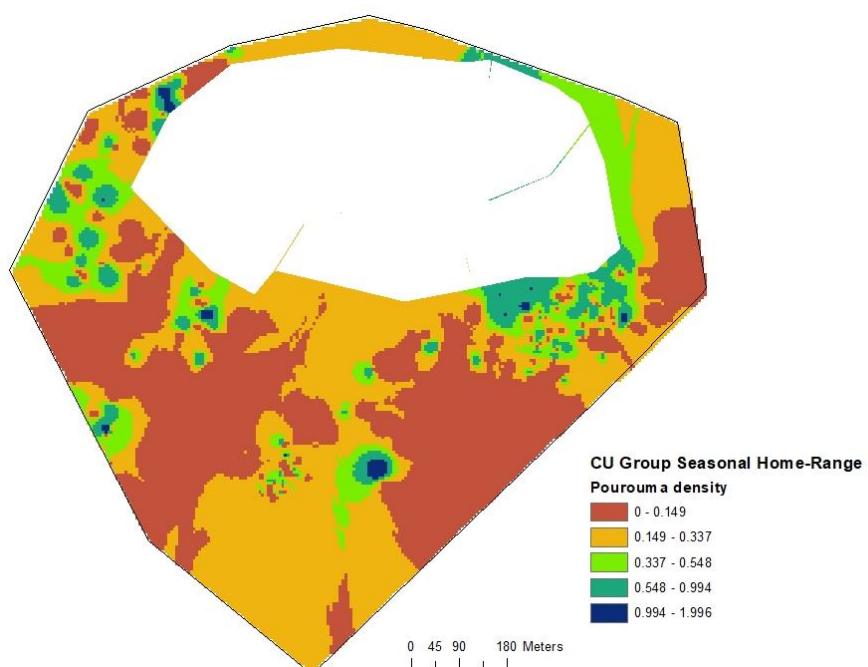


Figure 4.3. Annex. Kriging interpolation of Basal Area of fruiting trees sampled in the 15m X 15m parcels

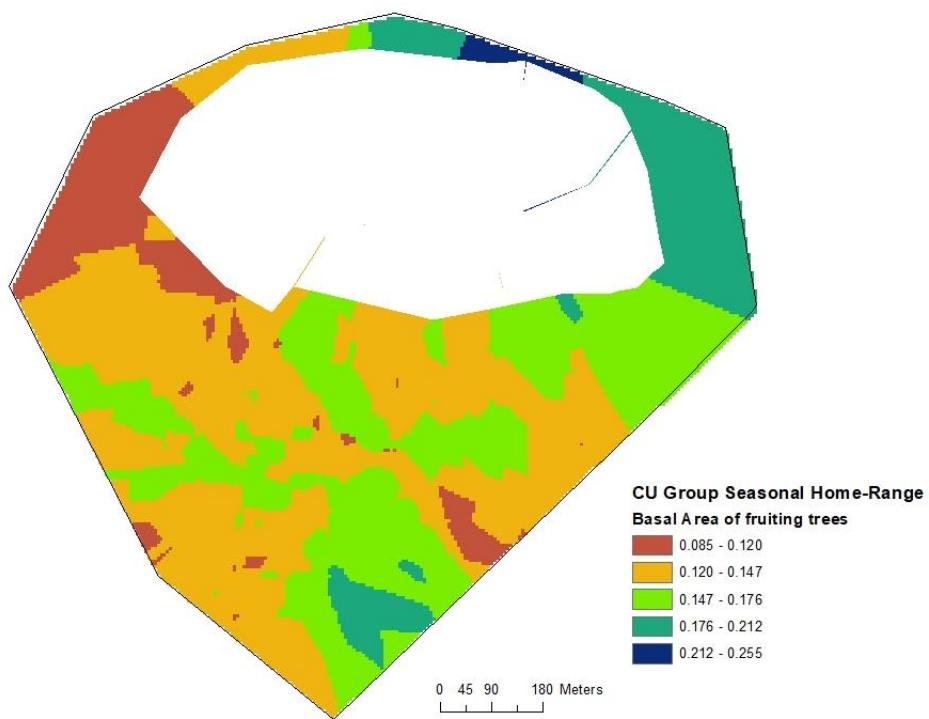


Figure 4.4. Annex. Kriging interpolation of Leaf Area Index of 15m by 15 m parcels within CU group seasonal HR

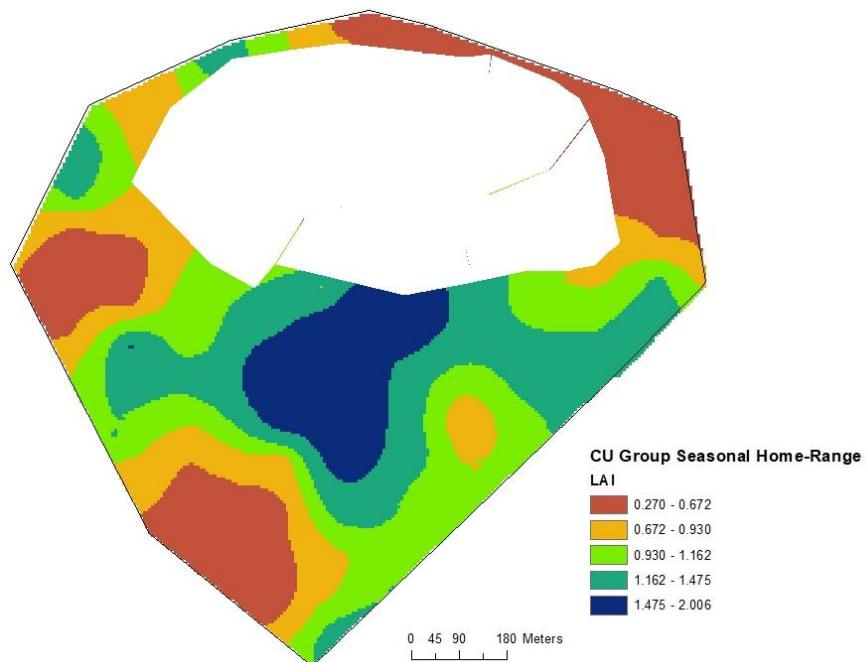
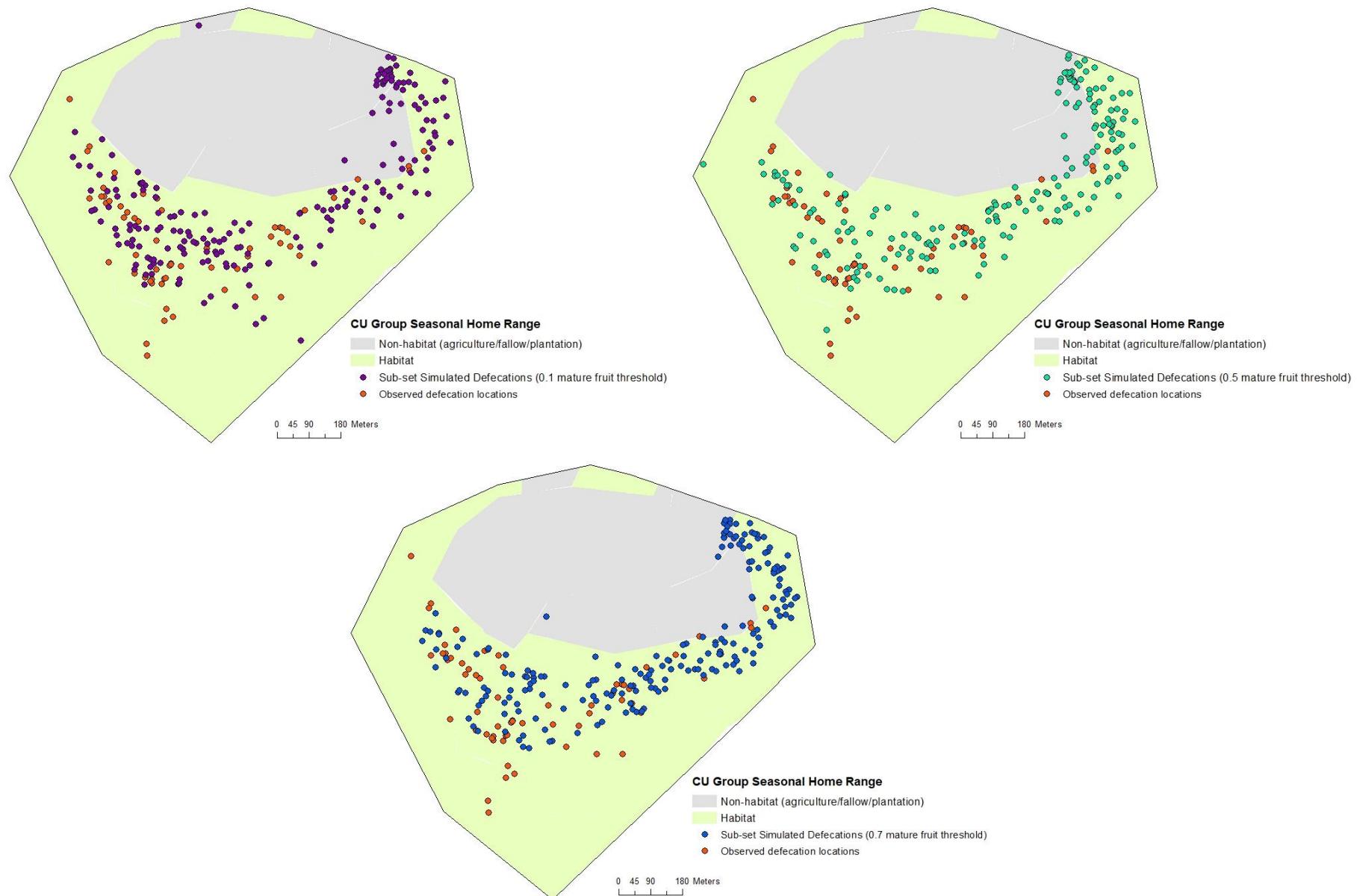


Figure 4.5. Annex. Simulated defecations from MOST, calculated with different Fournier score thresholds for *Pourouma* mature fruit availability



5 Model coupling and conservation applications

The tropical forest under threat

In countries where demographic pressure is high, damages to forest ecosystems occur at increasing frequency and intensity over time, to meet the economic development and the needs of more people. These behaviours are often correlated with a higher level of poverty. Decreased fallow time in slash-and-burn agriculture, excessive collection of forest products (plants and animals), logging, and land conversion (ranching with fire, permanent cultures) provoke, sometimes permanent, declines of forest cover and the fragmentation of the landscapes (Malhi et al. 2016). Export from the rural areas towards the cities, of a proportion of forest products for economic benefit, further increases the pressure on these already declining systems (Yadav et al. 2013; Kukkonen and Käyhkö 2014). In more developed countries like Brazil, and particularly in the BAF biome, permanent agricultural and agroforestry systems can coexist beside more or less degraded forest fragments. Independently of direct man-induced forest degradation, forest loss provokes biotic homogenization whereby the highly specialized taxa in many groups, such as trees, mammals, birds or insects, found in the forest cores are replaced by more common local species. The dominant hypothesis explaining these species turnovers is the so-called ‘edge-effect’. The newcomers take advantage of the proliferation of fire-degraded, dryer or more illuminated areas (Laurance et al. 2011; Pütz et al. 2011; Tabarelli et al. 2012).

In the core of the remnant forests, where the edge effect is not supposed to dominate, turnover affects also shade-tolerant tree species richness, and apparently does not favour shade-intolerant species (Pessoa et al. 2016). Beyond edge-effects, two mechanisms could explain the decline of tree richness: reduction of surface devoted to forest (species-area relationship), and disturbance of the seed dispersal processes (Shen et al. 2009). At a regional scale, tree species diversity seems preserved despite loss of abundances. It is likely that degraded habitats remain suitable habitats for many forest species, but mainly, tree longevity may conceal time-lagged responses (Joly et al. 2014). The rarest species, or those with limited dispersal ability, might be the first victims of this process. Concerning the second mechanism, dispersal barriers increase when forest cover decreases at the landscape scale (outside the forest cores) because the dispersing agents are no longer able to cross the deforested areas, thus impairing diaspore fluxes between forest patches. Seed size is a limiting factor, and in heavily defaunated areas, a lack of larger bodied frugivores may prove an important threat to migration, even if climatically suitable zones are available. Agroforestry intermediate habitats between forest patches could mitigate the consequence of deforestation (Bomfim et al. 2013).

Linking MOST and CARAIB

Identifying the factors responsible for biodiversity erosion and quantifying their relative importance is necessary to understand the potential benefits of different management or restoration actions, and use the limited resources allocated to conservation correctly (Smith et al. 2009). However, the capacity to infer the future by taking into account climate change remains limited, despite having several methods at hand. Among the options, dynamic vegetation modelling is a method of choice because it provides a platform to integrate processes and quantify complex interactions, within natural systems as well as within mosaic systems composed of forest patches, crops, or intermediate habitats (Fontaine et al. 2014).

In chapter 3, we demonstrated how using DVMs might be a more appropriate method to understand climate change impacts, particularly considering the habitats of restricted animal species. However, even DVMs have their limitations, notably to simulate dispersion in tropical areas, where zochory is the principal means by which plants can colonize areas, germinate, and eventually, survive. While climate change is, appropriately, a main focus in scientific research, the threat to biodiversity the most urgent to arrest is probably not climate change but habitat destruction. The scenarios leading to habitat conversion vary by region, and even country, and the specific social and economic contexts must also be taken into account when implementing conservation actions.

These are the reasons why we developed the Model of Seed Transfer (MOST), described in chapter 4, to simulate seed dispersal within the home-range of frugivorous animals, after observing the way GHLT disperse the seed of our focal tree species. This movement and dispersal model can be coupled with the CARAIB DVM, to capture the important effects of frugivory on vegetation migration. Essentially, the coupling of MOST with CARAIB can help understand the potential time lag for species to colonise new areas through zochory, though other on-the-ground conservation actions will still be required. Indeed, we have to address the mechanism of the coupling. Besides the general challenge on data availability relating to dispersal patterns by frugivores as input data for the dispersal module, another key challenge for the coupling is reconciling the different spatial scales between the typical DVM simulation and the frugivore trajectories.

Firstly, CARAIB is conceived as a global model mostly driven by climate and some soil factors, i.e. it computes plant growth independently for each of the several 60,000 cells of a grid spread over the continents. Differences in plant growth between cells occur mostly due to climate differences and marginally to soil differences. The available cells could be spread over smaller domains, for instance, over the area of the GHLT distribution, at a resolution of 1 sq. km, thus

furnishing what we could call a 'field of potential growth' of the selected tree species. The computational powers required for 1-km resolution for large biomes such as the BAF make such simulations time consuming, so a limit on the geographic scope is a necessary compensation for the higher resolution simulations. So far, we think that the scale of the animal movements (in its home-range, between trees) and of the processes of seed deposition, require an individual-based approach, i.e. the simulation of individual trees keeping their coordinates. Considering the fate of a set of seeds landing on precise coordinates on a particular grid cell, their chance to germinate could be evaluated, as well as their growth into trees, from germination time, i.e. biomass accumulation in the course of time could be computed for each potential tree desired to be simulated. This is actually possible using the CARAIB output of the grid cell, though CARAIB is not an individual-based model. We are also able to compute the fate of mature trees thanks to the field of potential growth, i.e. the potential future distributions identified by CARAIB, based on NPP.

Secondly, we need to be able to simulate the whole dispersal of the selected tree species, i.e. *Pourouma* does not rely exclusively on GHLTs, but are a part of a broader dispersal network. In chapter 4, we examined the seed dispersal of one genus, *Pourouma*, by GHLTs and demonstrated that GHLTs were mostly successful at short range dispersal; but, other animal species are effective dispersers of the genus and we were not able to collect data on other dispersers. We could hope or hypothesise that literature reviews might yield sufficient information to modify certain parameters within MOST, such as the configuration, variation of home ranges, the trajectories, or other constraining factors. Figure 4.1 in Chapter 4 shows the MOST algorithm, where parameters, obtained from HMM are used to trace movements, and data on gut-transit frequencies simulate dispersal. MOST can be improved by including other behaviours: in addition to frequency and duration of consuming fruits, territoriality, and predator responses, we should consider the phenology or seasonality of fruiting, and other behavioural aspects that may be relevant. For instance, aspects of social cohesion – fission-fusion movements will produce different seed shadows, latrine construction, birthing seasonality, etc. Additional behaviours linked to hierarchical fruit selection (Andrade et al. 2013), where some frugivores show specific preferences to certain fruits over others. Another layer of complexity includes data on secondary dispersal, by ants, dung beetles, rodents, etc. However, it is important to remember that these models are simplifications of real-world phenomena, and a scenario with 100% data availability is virtually impossible. In a review, Bello et al. (2017) demonstrate an important dearth in plant-animal interaction studies in the Atlantic Forest, citing biases in favour of certain taxa (mammals and birds), regions (southern range of BAF), and processes (primary dispersal). That review alone shows that even data on frugivores typically present in the GHLT distribution may actually be obtained from studies outside the BAF region and would necessarily represent a proxy for the GHLT range.

Thirdly, we need a landscape in which to simulate the seed deposition. Ecologists have often collected the conditions needed by the species to survive. For instance, Zeigler et al. (2010) calculated the minimum size of a forest fragment required to maintain a minimum viable population of GHLTs in their distribution, incorporating impacts of fire and disease spreading. But valuable information can also be obtained from studies quantifying species richness. Dalecky et al. (2002) showed that mammal species richness decline with the size of the forest fragments and the small fragments were mainly occupied by generalist herbivorous/granivorous species with small home-ranges in a French Guyana forest.

Were the data readily available for the GHLT distribution, the behaviour of frugivorous birds or bats, that could facilitate dispersal between fragments could be captured with HMM and parametrized in MOST. By overlaying movement trajectories for various taxa with CARAIB calculations of NPP, we can understand the likelihood of natural regeneration processes, assuming little to no anthropogenic disturbances. Few behavioural studies are available for phyllostomid bats and frugivorous bird species that are sympatric with the GHLT distribution (Faria et al. 2006). Nevertheless, studies from other regions can serve as proxy (Table 5.1) and might limit the uncertainties when parametrizing MOST for additional species. For instance, some species of toucans and the *Artibeus* genus of bats can visit feeding sources up to 10 km from each other in one day or night (Chapter 17 in Bongers et al. (2001)). Some frugivorous bats do not disperse seeds via defecation but have been observed to remove fruits and consume them from a perch hidden from potential predators, contributing to the seed's dispersal away from the parent canopy, but not necessarily having a physical or chemical impact to facilitate its germination (idem). Esbérard et al. (2017) studied movements of various bat species through capture-recapture experiments and showed that *Platyrrhinus lineatus* recorded a very large displacement, up to 120km with altitudinal displacement as well. This species is frugivorous, and found within the GHLT distribution (Faria and Baumgarten 2007), and could play a potential role in dispersing some pioneer BAF tree species between fragments. Parolin et al. (2016) suggest that spatial fidelity of some frugivorous bat species is linked to the phenology and occurrences of their preferred fruit species, which can have an impact on seed dispersal patterns as well.

Another species that may play an important role in dispersing *Pourouma* genus seeds is *Potus flavus* (kinkajou). Little data is available about the kinkajou from the BAF, except some studies confirming their presence (Miranda et al. 2018), plus limited personal observations in the field. Studies from French Guiana (Chapter 20 in Bongers et al. (2001)) show that almost 75% of observed faecal samples from the kinkajou contained seeds from *Pourouma bicolor*. Personal observations of the kinkajou in Colônia da Una saw an individual consuming fruit on a *P. velutina* tree. Kinkajous have home range sizes comparable to GHLTs, ranging from 20ha to more than 50ha (Kays and

Gittleman 1995). Kinkajous disperse seeds between 70 to 340m (average 200m, standard deviation 75) (Chapter 20 in Bongers et al. (2001)), similar to observations from GHLTs. Given the nocturnal behaviour, it can be possible for them to have complete sympatry with GHLT home-ranges without competition. However, based on the few studies that have observed their feeding and dispersal behaviour, we could suggest that kinkajous may in fact be functionally redundant with GHLTs, though their presence would contribute to more dispersal events, based on the similarities in their size and dispersal behaviours.

Table 5.1 Summary of potential *Pourouma* dispersers within GHLT distribution from “proxy” sites

Taxon/species	Body size	Potential or known disperser of <i>Pourouma</i>	Home range (hr) size and daily path length (dpl)	References	Other
<i>Potos flavus</i> (kinkajou)	Small bodied mammal	Known	20-53ha hr; no displacement data	Bongers et al. (2001) Kays and Gittleman (1995)	Average distance of seed deposited from parent tree 200m (range 70-340m; sd 75)
Phyllostomid bats (<i>Carollia</i> genus)*	Small bodied mammal	Potential	n/a	Bongers et al. (2001) Faria and Baumgarten (2007)	Better known for dispersing <i>Piperaceae</i> ,
<i>Artibeus</i> species	Small bodied mammal	Potential [¥]	n/a	Bonger et al. (2001)	
<i>Platyrrhinus lineatus</i>	Small bodied mammal	Potential	120km in capture-recapture study, not daily trajectory	Esbérard et al. (2017)	
Toucans	Small and medium bodied species, based on genus	Potential	From Amazon study site: mean MCP for two species: 191ha (<i>Pteroglossus</i>); 86ha (<i>Ramphastos</i>); estimated dispersal distance 270 to 450 m for medium-seed size	Holbrook (2011)	Little data available for northeastern BAF

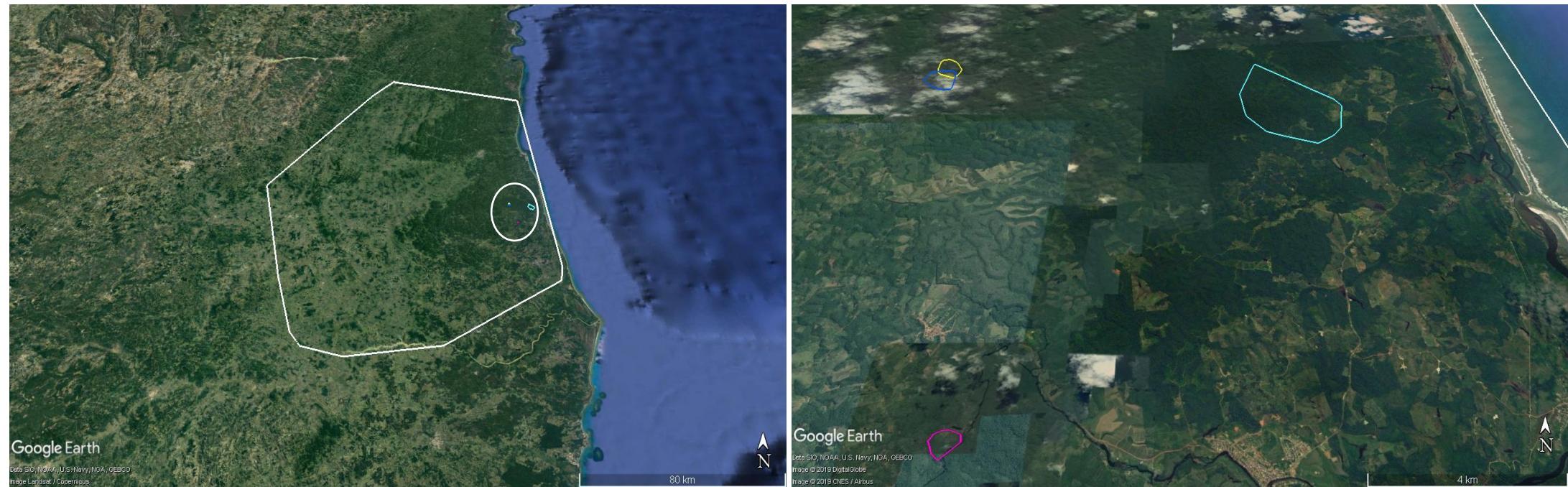
*These species are present in the same range as GHLTs, but my bat sightings in *Pourouma* trees did not permit any identification of species

[¥]Bongers et al. (2001) described behaviours linked to fruit removal and consumption on perches some distance from the parent tree, rather than defecated dispersal, for larger seeded fruits.

In a study on habitat loss effects on frugivory in southern Bahia, corresponding largely to GHLT distribution, Menezes et al. (2016) identified 49 species of frugivorous birds, with declining abundances of species associated with forest interiors. This may imply that there is a higher likelihood of seed dispersal outside home-ranges of GHLTs by edge-species, though body size will play a cardinal role in the dispersed tree species, while conditions in the dispersed site may not always support germination and survival. The complex interactions between species movements, trajectories, home-range sizes and their preference or not for edges was observed in the *Turdus* genus by Da Silveira et al. (2016). Their study reinforces the need to integrate or account for various frugivore profiles into landscape simulations, in order to better inform decisions on areas for natural regeneration vs. active restoration.

MOST itself can be run in parallel for several animal species, and each year, we can select a subset of the defecated seeds which will germinate and survive using the conditions and the NPP obtained from CARAIB, which will drive the growth. However, it can be rather complicated to build maps of home-range configuration and distribution for each of the dispersing species over BAF or over an area large enough to infer the survival of a tree species like those of the genus *Pouroversa*. If we consider in Fig. 5.1 the right-hand image, the known distribution of GHLTs is overlaid on a 2019 google earth pro image, and the small, insignificant shapes (zoomed on the left image) represent known home-ranges of three groups of GHLTs and one group of Sapajus. With known arboreal species, trajectories simulated using MOST will likely not venture into potential areas that could be colonised, outside of forest fragments. This still leads to the question, “How can home-ranges or movement trajectories be plotted?”. Biogeographic databases like GBIF contain coordinates of focal dispersing species but the home-range or movement data are lacking. Thus, rather than trying to simulate within the current framework, which lacks data of satisfying precision, we propose to examine systematically various hypotheses of home-range distribution with more or less connectivity between them, using literature and biogeographic databases to fix the limits of hypotheses. Running the models under various hypotheses could provide thresholds in forest density and distribution, level of connectivity and animal species occupancy, which would allow the long-term survival of the selected tree species and by this way, would delineate the possible futures of the focal tree species under a set of hypotheses over animal densities and forest fragmentation.

Figure 5.1 Google Earth images with known distributions of GHLTs (left); and known home-ranges for three GHLT groups and one *Sapajus* group within the GHLT distribution (right; bottom left in pink outline, Colônia da Una group (2014-15); Overlapping blue and yellow, top left are two groups from Una Biological Reserve (2006 data), and top right is a *Sapajus* group (2013)). The image on the right has zoomed in on the white circle outlining the locations of the studied primate groups within the GHLT distribution.



Conclusions and conservation strategies

Thus far, we presented the possible impacts climate change could have on several tree species in the Brazilian Atlantic Forest and explored whether GHLTs could help or hinder any potential migration towards appropriate climates, using one model tree genus, and one frugivore.

Based on the MaxENT modelling results, the following species are at risk of losing more than 90% of their original distribution with climate change: *Anomospermum reticulatum*, *Artocarpus heterophyllus*, *Brosimum rubescens*, *Calyptranthes lucida*, *Cheiloclinium cognatum*, *Cordia bicolor*, *C. nodosa*, *Diospyros hispida*, *Guettarda viburnoides*, *Microphilis guyanensis*, *Micropholis venulosa*, *Pourouma guianensis*, *P. mollis*, *Pouteria bangii*, *Protium aracouchini*, *Rheedia macrophylla*, *Simarouba amara*, *Sympodia globulifera*, *Zanthoxylum rhoifolium*. CARAIB's more optimistic simulations yielded no more than a 10% loss in the original distributions of the same. Additionally, the endemic species, which were not considered in the MaxENT simulations, but simulated in CARAIB, that are at risk of losing at least 50% of their original distribution includes *Manilkara maxima* and *Pradosia lactescens*. Many of the species whose simulations suggested more than 50% loss in the original distribution are middle to late successional species, rather than pioneers. The warning, as explained earlier with the challenges in presence-only modelling, is that there could be an important underestimation of their potential distributions, because the known presence may not reflect the full potential range, and will bias statistical modelling. However, using the precautionary principle for conservation decision making, the potential losses in distributions are important. For these species, their average seed size requires medium to larger bodied frugivores, precisely those animal species that are the first to disappear due to hunting pressure, leaving the tree species doubly at risk. As evidenced in Bogoni et al. (2018), the levels of defaunation for frugivores are quite high, and within the GHLT range, their kriging of defaunation index is within the moderate to intensive levels of defaunation.

The principal conclusion, based on the predicted impacts of climate on the species as listed above, the levels of defaunation, and habitat loss in the BAF biome implies that conservation actions, both in the field and at policy levels are mandatory for the conservation and functionality of the BAF despite the fact that large uncertainties remain on the effect of climate change when comparing MaxENT and CARAIB results. Bogoni et al. (2018) calculated a “defaunation index” for the BAF, confirming that apex predators (carnivores) and generally, large bodied mammals, including frugivores were conspicuously absent in large parts of the biome. Their research correlated this loss with vegetation cover, fragment size, and distance between factors – i.e. habitat loss – with these alarming trends. In fact, their research cites that in the biome, primates are the most endangered taxon,

relative to other mammalian taxa. Further research on loss of functional redundancies in other taxa would likely see similar trends, contributing to the empty forest scenario. The section below explores some strategies relevant to conserving the BAF, and hopefully much of its associated fauna and vegetation.

Restoration and natural regeneration

With the loss of dispersal services that succeed defaunation in tropical areas, regeneration processes in forested areas are limited. Another important factor that affects regeneration is recruitment limitation linked to habitat loss, which can be exacerbated by changes in the microclimate. A restoration or natural regeneration strategy can be designed taking into account connectivity between forest patches (Tambosi et al. 2014), as well as selecting native species. Some active restoration or natural regeneration projects have demonstrated the re-colonisation of these areas by fauna – therefore, the strategy can engender many benefits – increasing the habitat available for fauna threatened by habitat loss (Santos Junior et al. 2016), sequestering carbon dioxide, as well as a host of other known services linked to native forest cover.

There are however a few challenges to implementing a restoration/regeneration strategy. Not all native species are uniformly easy to germinate ex-situ for nurseries, and sometimes the processes for acquiring seeds requires effort. Additionally, the soil conditions in areas may require prior treatment, depending on the nature of its previous conversion (Elliott and Kuaraksa 2008). Besides challenges linked to the growth of species of interest, there are social considerations that must be taken into account. Land zoning and titling processes must be put in place with local community members and land owners to ensure that there is no encroachment or expropriation of areas. A socially inclusive approach can render more success in the long-term maintenance of restored or regenerated areas (Kerby et al. 2000). However, even with the most socially inclusive policy for restoration, this is a costly strategy. Brancalion et al. (2012) estimated that costs for active restoration in the BAF area at 5,000 USD per hectare, which includes the opportunity costs from unsustainable conversion activities (such as cattle ranching). In Brazil, considering the distribution of the GHLTs particularly, one way of benefitting the local communities is working on agro-forestry systems, with cacao and other fruiting trees that can provide sources of income. The income from agro-forestry systems, coupled with other payment mechanisms may help offset the initial investment costs towards “forest-friendly” economic activity. We noted however that the long-term survival of the cacao *cabruca* system has been questioned and that its role in maintaining biodiversity in the long term could be limited (Rolin and Chiarello 2004) and better practices for biodiversity conservation would have to be implemented. In Bolivia, Kew gardens worked with local communities to use the *Inga edulis* in agro-forestry systems for crops besides the conventional cacao and coffee. *Inga* species provide shade for the crop bat are

known “attractors” of frugivores. Such areas can serve as corridors to maintain connectivity between forest patches. Monro et al. (2016) produced an agro-forestry manual describing the restoration and agro-forestry techniques applied in Bolivia using *I. edulis* for soil restoration. GHLTs as well as other frugivores, such as toucans, sapajus, tapirs, etc. consume the fruits of *I. edulis*. In Brazil, *I. edulis* could be used to capture a site, and planting keystone or other native vegetation in between dense rows, to promote regeneration of degraded areas. De Oliveira and Carvalhaes (2016) identified 92 species of trees that could be viable in agro-forestry systems in the BAF area, breaking down the type of use as well as other functional traits that could be harvested. It may be relevant to test site capturing with several species, rather than *I. edulis* alone, to offer a level of diversity to the communities.

Natural regeneration may be less costly, depending on how land is acquired for the process. In such an instance, there may or may not be a connectivity component, as it is a “hands-off” technique allowing fallow or unfertile areas to slowly recover vegetation through all the succession processes. However, Sansevero et al. (2011) demonstrated, in the habitat of the *Leontopithecus rosalia* (Golden Lion Tamarins), that natural regeneration processes in areas that were converted for pasture and maintained with fires benefit from some planting to catalyse the regeneration process. This may be relevant for the GHLT distribution as well. Planting to catalyse regeneration is also known as assisted regeneration. In Zahawi et al. (2013), they tested an applied nucleation method in Costa Rica, demonstrating that this method, (a form of assisted regeneration) may be a more economical option in large-scale restoration efforts. Elliott and Kuaraksa (2008) applied the same kind of approach in Thailand.

In concrete terms, there are not as many studies focusing on the tree species particularly identified in this research (and mentioned at the beginning of this section), but more broadly linked to climax, late successional, and pioneer species. In an experiment on direct seeding, Bonilla-Moheno and Holl (2010) demonstrated that for some late succession species (including a *Manilkara* species), there is evidence of seedling survival in fallow plots abandoned for at least 8 to 10 years. This could be a potential strategy for promoting regeneration, particularly for the species identified from the MaxENT and CARAIB simulations that risk losing large parts of their original distribution.

The IUCN published a cost-benefit toolkit to help decision-making around forest restoration strategies (Verdone 2015). Presenting decisions on restoration framed around such analyses, or using models like InVEST, can help provide arguments to key decision-making stakeholders on the viability of a restoration or assisted regeneration strategy. Indeed, Calmon et al. (2011) demonstrated the importance of restoring parts of the BAF, increasing the forested area to at least 30% of the original distribution. Currently, there is a coalition of more than 260 stakeholders in an “Atlantic Forest Restoration Pact” (AFRP; *Pacto pela restauração da Mata Atlântica* in Portuguese), which aims to

restore 15 million hectares (of the original 1.2 km²) in the BAF by 2050, with clear annual monitoring plans established. In Pinto et al. (2014), they indicate that the Bahia state, has a potential 2,104,511 ha, compared to its original area of 18,955,797 ha, that can be restored, as part of the pact. With 33 organisations participating in this pact for Bahia, there can be viable conservation for fauna in the BAF, including the GHLTs.

Sustainable hunting and BAF rewilding

The consequences of defaunation have been well documented. Loss of larger-bodied animals, particularly frugivores, leads to disruptions in seed dispersal processes and engenders risks to regeneration in natural ecosystems. In the BAF region, particularly in defaunated areas where frugivores have all but disappeared, it is no longer viable to rely on natural processes and recommend active restoration and policy enforcement measures to combat habitat loss and the consequent demise of fauna. Sustainable hunting and rewilding can be vital on-the-ground strategies, to increase the efficacy of the other two mentioned above.

Hunting is typically a subsistence activity in the BAF areas, as a source of food principally (de Souza and Alves 2014; Castilho et al. 2018), though hunting for pets, medicine, and trade can be important in some regions, particularly threatening bird and reptilian taxa. In some areas, sport or recreational hunting also exists (de Souza and Alves 2014). Addressing illegal, and unsustainable hunting will require several components: Enforcement (park-guards in protected areas, who are trained on legal issues, and fully equipped); environmental education (for both children and adults), and in the case of indigenous peoples, developing sustainable hunting management plans, that can restrict the age, size, number of individuals, and seasonality of hunting based on the biology of different species of interest. The key species hunted in Bahia are armadillos, peccaries, deer, paca, and unsustainable hunting locally extirpated species like tapirs, white-lipped peccaries, and birds like macaws (Flesher and Laufer 2013). Castilho et al. (2018) particularly showed how peoples' attitudes towards conservation or protected areas correlates with their hunting behaviour. Raising awareness on the importance of local, native fauna, and the roles of protected areas and sustainable land uses may be the best long-term strategy to address unsustainable hunting. Enforcement through sanctions may have some efficacy. de Azevedo Chagas et al. (2015) documented the seizures of illegally hunted animals by surveying the Brazilian military and police forces. While Bahia state did not participate in the survey, this research demonstrates the high potential to monitor illegal hunting and even test the efficacy of hunting measures by collaborating with seemingly unlikely agencies, such as the police and military forces. This will need to be complemented with other measures and monitoring techniques for local, subsistence hunting.

Rewilding can be also an effective strategy. Sobral-Souza et al. (2017) demonstrated that rewilding some habitats in the BAF with small tortoises (*Chelonoides carbonarius* and *C. denticulatus*) could potentially replace the functions of other frugivores. This strategy could have an advantage in forest patches that are too small to host native fauna, until connectivity or restoration increase availability of suitable habitat. Nevertheless, rewilding is an extremely difficult strategy. Successful examples of primate reintroductions are few. Surprisingly, in Rio de Janeiro, *L. rosalia* has been somewhat successfully reintroduced to Poça das Antas reserve (Beck et al. 1991). Of course, with increasing fragmentation of the forest areas, even if a sufficient number of captive or wild-born GHLTs are present for reintroduction in Southern Bahia, there may be lower rates of success, as the Una Biological Reserve in Bahia is the last large fragment remaining in the GHLT distribution, and it may already be at carrying capacity. Oliveira et al. (2010) show that under some management options, shade-grown cacao areas can be suitable habitats for GHLTs. As a strategy for connectivity between patches, this may be viable, but actively diminishing hunting of other key BAF fauna will be critical to restore functional diversity as well. Fortunately, smaller bodied primates are not at high risk for hunting, except for pet traffic, so frugivorous primates are most impacted by habitat loss.

Restoring functional diversity will be more challenging. Rewilding experiments have been conducted in parts of the BAF. Galetti et al. (2016) presented rewilding through restoration of trophic food chains as a potential strategy to compensate for defaunated areas, and to restore functional components of BAF areas. Fernandez et al. (2017) realized an experiment on rewilding or reintroduction of two seed dispersers (agouti and howler monkeys) in a national park in Rio de Janeiro to test whether ecological interactions could be restored. The main hindrances – barring the ability to acquire source populations – in the project were less linked to the capacity of the animals to re-adapt to a wild environment and more similar to the challenges faced in managing resources within natural ecosystems (protected or otherwise). As strategies go, if source populations of key species could be available, by overcoming mostly administrative challenges in the acquisition of genetically appropriate individuals, then rewilding or refaunation could be a viable strategy. Ideally, while individuals are being collected or trained for reintroduction, on-the-ground actions preparing communities, hunters, and other key stakeholders to desist in unsustainable activities would be vital. Additionally, a suitable area of the GHLT distribution may need to be restored to receive apex fauna and key elements of functional diversity.

Policy measures

Some very interesting deforestation dynamics have been recorded in the BAF, since monitoring began in 1985. The NGO *Fundaão SOS Mata Atlântica*, (SOSMA) was founded in 1986 with the objective of conserving the BAF. They recently published a comprehensive report on

deforestation trends in the BAF states since 1985. The average annual deforestation within the BAF decreased from 107.3 ha in 1985 to 12.6 ha in 2017, with 7 BAF states with almost zero net deforestation. In 2017, following an alarming year where Bahia had seen a 207% increase in deforestation in 2016, compared to the previous year, the state led on the charge to decreasing it's deforestation by 56% (SOSMA 2017). The year with 207% increase in deforestation had southern Bahia contributing up to 30% of that rate, particularly citing Ilhéus and Porto Seguro as the administrative units to blame. While the report did not cite the cause for this, one can reasonably speculate urban expansion leading to this result. A similar reversal in trends (high rates in 2016 and important decreases in 2017) was also observed in the states of Minas Gerais and Paraná. This suggests that there can be immediate and observable effects of on-the-ground and policy actions. However, it is very important to ensure that the decreased deforestation rates are a genuine reduction, rather than an artefact of too little forest remaining to be exploited.

While the two previous strategies demonstrate on-the-ground conservation actions, this looks to laws and legislations. On the policy side, Brazil could develop an equivalent pledge for the BAF as it did for the Legal Amazon (reduce gross deforestation in the Legal Amazon by 80% below mean levels of 1996-2005 by 2020; http://www.planalto.gov.br/ccivil_03/_Ato2007-2010/2010/Decreto/D7390.htm). This can complement the AFRP by diminishing conversion in the first place. Additionally, newly restored or regenerated areas can be legally recognized as corridors or protected areas, which can confer some degree of protection against future conversion. Facilitating policies for community members to implement sustainable agricultural practices can also stem some of the threats to the BAF, and hopefully provide suitable incentives against conversion.

Brazil could also learn from its neighbour – Paraguay implemented an Atlantic Forest Zero Deforestation Law in 2004, forbidding conversion in the eastern part of the Atlantic Forest within Paraguay. Satellite monitoring in the zone shows at least an 85% decrease in deforestation rates, from 88,000-170,000 hectares annually prior to the law, down to ~ 16,700 ha per year (Hutchison and Aquino 2011). At 56% decrease in deforestation reported for the BAF region, Brazil could reach Paraguay's success with little added effort.

Brazil's compensation laws are designed for companies to mitigate their environmental impacts but have not been uniformly implemented. The Forest Compensation Law (*Lei de Compensação Florestal no Distrito Federal*, Decreto n°23.510 de 31 from December 2010) has been critiqued for its high costs and lack of effective guarantees for environmental protection. In view of these challenges, the Federal District Environmental Secretary has proposed a new forest compensation law. The key difficulty in implementation has been calculating ecological equivalence – an area restored or protected that is equivalent to the areas being converted, accounting for

environmental service and social justice, and not exclusively in terms of volumes or species of vegetation (Gasparinetti et al. 2017), which the new law proposes to address. Thus far, under the current legislation, the enforcement, finance, and reinvestment structures do not appear to have sufficient capacity to successfully reinvest funding for conservation (Geluda and Young 2004). There have not been examples of successful offset mechanisms, mostly due to the issues around compliance, even when equivalence has been addressed (Bull et al. 2013). Overall, as legal mechanisms go, environmental compensations should be applied with care, and more as a source of revenue towards conservation activities (protection, working with local communities, etc.) than its usefulness in mitigating damages due to conversion.

Policies are often only as effective as the economic analyses demonstrating the benefits of conservation. Private sector companies wield financial arguments to push forward activities, which traditional environmental impact analyses are unable to dissuade. The Natural-Capital (NatCap) programme develops tools (like InVEST) to conduct economic analyses including costs of potential losses of ecosystem services that can offer governments and other decision-makers more information regarding private sector investments in natural ecosystems. InVEST allows decision-makers to assess quantified trade-offs associated with alternative management choices and identify zones where investing in natural capital can enhance human development and conservation. The tool is applicable in terrestrial, freshwater, marine, and coastal ecosystems, with additional modules to help interpretation and visualisation of outputs. In a future research phase, combining outputs from DVMs like CARAIB with management scenarios in tools like InVEST could help improve assessments on risks to terrestrial ecosystems under different climate and management contexts (Sharp et al. 2018). Coupling improved enforcement on existing laws, social inclusiveness and working with local communities, with improved economic analyses, effective conservation of the BAF ecosystem can still be achieved.

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