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Parameterization, Development and Ecological Implications of a Seed Dispersal Model by Howler Monkeys

by

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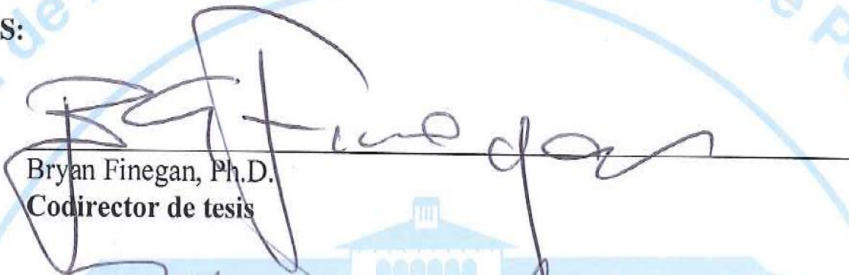
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II

DEDICATION

I'd like to dedicate this thesis to my parents, Mary Helen Bialas and Ronald Rivera, for their unconditional love and support throughout my life, for their trust, and for pushing me to fulfill my studies and to be a better professional. To Tadeo Camacho, for his constant love and emotional support during this process, his wonderful words of encouragement and boosts of confidence when most needed. To the good friendships developed over these years of communion in CATIE, for all laughs and sentimental moments we sheared. To all who contributed with their knowledge and experience during the development of this investigation. And to myself, for concluding this challenge of great expectations with content and satisfaction.

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3. LIST OF ACRONYMS, ABBREVIATIONS AND UNITS

LDD: Long-Distance Dispersal

GRT: Gut Retention Time

CC: Climate Change

SINAC: National System of Conservation Areas of Costa Rica

NP: National Park

HR: Home Range

MCP: Minimum Convex Polygon

4. RESUMEN

El estudio de la dispersión de semillas es crucial para la comprensión de procesos de importancia ecológica para la dinámica de poblaciones, que a su vez se relacionan con servicios ecosistémicos como el reclutamiento y la restauración ecológica, la migración de plantas en respuesta al cambio climático histórico y futuro, y el sostenimiento de la biodiversidad. En la actualidad, la proyección de cambios en la distribución y composición de las comunidades vegetales en respuesta al cambio climático es una de las más grandes causas de la investigación debido a que estas respuestas pueden tener un gran impacto en la dinámica futura de los bosques, la estructura, la biodiversidad y el secuestro de carbono. Así, el movimiento de las poblaciones vegetales a través de paisajes es el resultado de la dispersión de semillas (entre otras condiciones); y la integración de la dispersión local y de larga distancia, es esencial para predecir las tasas de migración de la vegetación. Sin embargo, la mayoría de los modelos que tratan de predecir la futura distribución de las poblaciones de plantas no incluyen el proceso de dispersión de semillas.

Los valores de dispersión de semillas, especialmente los valores de dispersión a larga distancia, aunque de vital importancia para la dinámica a gran escala de las comunidades vegetales, son difíciles de implementar y medir empíricamente. Es por ello que esta área de investigación se ha dirigido con el uso de modelos matemáticos de simulación que ayudan a predecir dichos valores, ya que los modelos requieren más supuestos que datos empíricos y, por tanto, se aplican fácilmente. Sin embargo, pocos de estos estudios han adoptado este enfoque utilizando la endozoocoria como medio de dispersión de semillas debido a su gran complejidad conceptual.

En este sentido, los monos aulladores representan un buen sujeto de estudio, ya que son uno de los más grandes primates del neotrópico, y por lo general muestran las mayores densidades poblacionales entre los primates; además, la proporción de fruta en su dieta es de 10-60%. Los monos aulladores son a menudo los únicos agentes de dispersión de semillas de gran tamaño que pueden sobrevivir durante mucho tiempo en pequeños fragmentos de bosque y por lo tanto pueden jugar un papel crucial en los procesos de regeneración del bosque. Por lo tanto, las interacciones entre las especies de primates y la comunidad de plantas son muy importantes para la conservación.

Nuestro modelo *MonkeySeed* representa un enfoque para el estudio de distancias y patrones de dispersión de semillas para monos aulladores del género *Alouatta*. En general, este modelo representa un enfoque metodológico para el estudio de la dispersión de semillas a través de mamíferos por endozoocoria, ya que incluye muchos factores intrínsecos (tiempo de retención intestinal, el comportamiento, las actividades diarias de los monos) y extrínsecos (abundancia y distribución de árboles con frutos, tamaño de semillas ingeridas) que permiten obtener respuestas a preguntas de importancia ecológica. Este modelo es el resultado de una extensa revisión de la literatura, trabajo de campo, que en conjunto proponen una herramienta para entender mejor su contribución en la lluvia de semillas de los bosques tropicales de la región.

Palabras clave: monos aulladores, modelo de dispersión de semillas, dispersión a larga distancia

5. ABSTRACT

The study of seed dispersal is crucial for understanding processes of ecological importance of population dynamics, which in turn relates to ecosystem services like recruitment and ecological restoration, plant migration in response to historical and future climate change, and maintaining biodiversity. Currently, predicting changes in expected distribution and composition of plant communities and species in response to climate change is a key area of ecological research, because these responses can have a big impact on future forest dynamics, structure, biodiversity, and carbon sequestration. As it is, the movement of plant populations through landscapes is a result of seed dispersal among other ecological processes; and integrating understanding of local dispersal and long-distance dispersal, with the natural history of the species, is essential to predict migration rates of vegetation. However, as important as it is, most models that attempt to predict the future distribution of plant populations don't include the seed dispersal process.

Seed dispersal distances, especially long-distance dispersal values, though crucially important for large-scale dynamics of plant communities, are difficult to measure empirically. That is why this aspect of research has been incorporated with the use of mathematical simulation models that help predict outcomes for seed dispersal, because models require more assumptions than empirical data and therefore are applied more easily; however, few modelling studies have embraced this approach using animal-induced seed dispersal because of its great conceptual complexity.

In this regard, howler monkeys represent a good prospect for seed dispersal research, since they are one of the largest Neotropical primates, and they generally show the highest density among primate populations; also, the proportion of fruit in the howler diet goes from 10 to 60%. Howler monkeys are often the only large-bodied seed dispersal agents that may survive for a long time in small forest fragments and thus may play a crucial role in plant regeneration processes. Therefore, interactions between the primate species and the plant community are highly relevant to conservation purposes.

Our *MonkeySeed* Model represents an approach for the study of long-distance dispersal and the general dispersal patterns of howling monkeys. This model has been parameterized for howler monkeys of the *Alouatta* genus, to better understand their contribution to seed dispersal shadows in tropical forest of the Neotropics. Overall, this model represents a methodological approach for the study of mammal seed dispersal through endozoochory (ingested and excreted seeds), as it includes many intrinsic factors (gut retention time, behavior, daily activities) and extrinsic factors (tree abundance and distribution, and seed-size) of the species that need to be taken into account to help answer important questions concerning the resilience of tropical forests. This model has been parameterized through literature review and field work, and is a promising tool for the study of endozoochorous seed dispersal.

Key words: howler monkeys, seed dispersal model, long distance dispersal

6. INTRODUCTION

6.1 Background

Debate generated around the issue of tree dispersal has concentrated on the migration of canopy tree species; as it is, these species have been generally better represented in the global paleo-ecological record (Pakeman 2001). So, based on studies conducted with paleo-ecological records of the Holocene, the "fast post-glacial migration model" became widely accepted, even though it contradicts current understanding of dispersal tendencies based on the natural history of the species, and it has been explained based on stochastic events of long-distance dispersal (Clark 1998, McLanchlan 2005). However, it has recently been shown that migration rates are slower than thought (under 100m/year, McLanchlan 2005, Pearson 2006); this results has substantial implications for the capacity of response that was believed tree species possessed for contemporary climate change.

As it is, in recent years the growing recognition of the importance that the study of seed dispersal over long distance (LDD) represents for tree species has become evident, because of their close relationship to ecological processes and evolutionary population dynamics (Nathan 2006, Nathan et al. 2008, Schupp et al. 2010). This research area has been integrated with the use of mathematical simulation models, that mainly focus on seed dispersal by wind as a LDD mechanism (Hovestadt et al. 2001, Soons et al. 2004, Katul et al. 2005 Soons and Ozinga 2005, Soons and Bullock 2008, Rosindell and Cornell 2009).

According to Higgins and Richardson (1999), prior studies on the migration of flora have relied on measuring the effects of population growth, the distribution of opportunities for recruitment, and loss of habitat due to fragmentation; and while recognizing the important role of seed dispersal in these different population dynamics, statistical methods available have limited modeling to describe seed dispersal in forests in simple, "realistic" terms. This is mainly due to the difficulty of including LDD events, so the models that have been developed tend to use harsh functions that either aren't explicitly linked to data (with varied criteria of parameterization according to the study) or the use of short-tailed data functions which account for only local dispersal, (Higgins and Richardson 1999).

Seed dispersal as such has been a topic fairly investigated from different perspectives in ecology (Schupp et al. 2010). For the study of the movements of the diaspora (dispersal units of plants), ecologists have used different techniques for tracking and relocation, mainly through (Shea 2007): direct observations of dispersal agents in the mother plant; the study of environmental conditions which promote the release of wind dispersed seeds; the use of seed traps at different distances from the parent source; seed labeling using ink, fluorescent powders or radioactive markers that allow the subsequent collection and identification of seeds; also genetic methods to link the seed or pollen parent have been used; and following the trajectories of individual seeds as they fly through a landscape.

In the case of howler monkeys, the method mostly used to study their seed dispersal has been tracking and observing family groups and the collection of dung to obtain gut

retention time and diet information, spatial patterns of seed deposition, and overall seed dispersal information (Estrada y Coates-Estrada 1984, Julliot 1996, Yumoto et al. 1999, Bravo and Sallenave 2003, Martins 2006, Bravo 2009, Amato and Estrada 2010); also recruitment of certain tree species under latrine and non-latrine sites can be counted, and forest fragments with or without howler monkeys studied to determine to study the impact of their seed dispersal in the regeneration of the forest (Julliot 1997, Anzures-Dadda 2011, Bravo 2012). A different approach in the study of seed dispersal by howler monkeys is to focus on secondary dispersal by dung beetles, with the use of different experimental seed removal techniques (Estrada and Coates-Estrada 1991, Andersen 1999, Andersen 2002, Ponce-Santizo 2006). Regardless of all research generated on howler monkey seed dispersal, little advances have been made on LDD values and their contribution for canopy tree migration capacity.

6.2   Importance

Looking at the large investment of energy that plants use in creating diversity of sizes, shapes, colors and aromas of fruits and seeds, and the variety of rewards that are offered by plants to the range of agents that disperse them; one can sense that seed dispersal plays a central role in plant ecology (Howe and Miriti 2004). In fact, most plants in tropical forests have evolved to require the presence of animals for the successful dissemination of their seeds, forming various types of mutualism with frugivorous and granivorous animals; animals have thus become dispersal agents and play a crucial role in the structure and regeneration of many forest tree species (Nasi et al. 2002).

Seed dispersal is an important ecosystem service that can be classified as a support service, like pollination (MEA 2005). The future of ecosystem services under climate change is uncertain, and although in tropical regions changes are expected in the structure and composition of forests (Lorente et al. 2004), little is known about possible consequences for these complex services. The study of seed dispersal is crucial for understanding processes of ecological importance of population dynamics, which in turn relates to ecosystem services such as limitations for recruitment and ecological restoration, plant migration in response to historical and future climate change, maintaining biodiversity, the ecological consequences of fragmentation, and the effectiveness of biological corridors for conservation (Schupp et al. 2010).

Chazdon et al. (2009) assert that one of the priorities in the research agenda for conservation biology should be "modeling of potential impacts of climate change on biodiversity and species migration through modified landscapes". Indeed, "to predict changes in expected distribution and composition of plant communities in response to CC is one of the largest areas of ecological research today, because these responses can have a big impact on both the future of biodiversity and carbon sequestration of forests" (Corlett 2009).

In this sense, according to Higgins and Richardson (1999) "the movement of plant populations through landscapes is a result of its population growth, seed dispersal, the availability of optimal conditions for seedling recruitment, and landscape structure"; this is why "integrating local dispersal and LDD with the natural history of the species, natural and

anthropogenic disturbances, and variability of habitats is essential to predict migration rates of vegetation" (Higgins and Richardson 1999) .
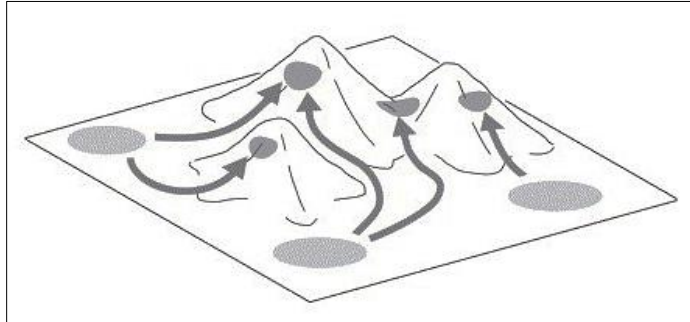
Fig. 1 Graphical representation of migration in an altitudinal gradient of a tree species.

Currently, CC and habitat destruction are recognized as the greatest threats to the survival of biodiversity; and as a result, it is expected that the fauna and flora will migrate to new landscapes at higher elevations (Chazdon et al. 2009, fig. 1). That is why in order to predict the ability of species to adapt and survive in different areas, migration capability is necessary to have knowledge of how individuals move or disperse through the landscapes, how they choose habitats for their development, and how to produce offspring that survives and repeats the process (Knowlton and Graham 2010). Consequently, the study and understanding of seed dispersal is critical to analyze the behavior of plant populations over time in changing ecosystems, and together, changes in distribution of animals accompanying tree species.

6.3   Justification

Because of the extent of the loss of natural habitats do to fragmentation and CC that rule out important ranges that can play part in potential habitats for species, there is considerable uncertainty whether the migration capability of tree species will allows the colonization of remote areas that can become favorable for their establishment in the future (Clark 1998). CC has already generated detectable impacts on global biodiversity, threatening the long term survival of the species, communities and services that are offered by biodiversity to people. Some CC impacts are manifested in altered phenological cycles, density and population structure, and have also detected changes in home ranges of species (therefor correlated with dispersal processes). Seed dispersal has become the very core in predicting changes in the distribution of species in response to CC, which has become an important goal in Ecology, and greatly facilitates the understanding and development of adaptation and migration strategies for the conservation of biodiversity (Brooker et al. 2007)

As important as it is, according Vittoz and Engler (2007), most models that attempt to predict the future distribution of plants don't include the seed dispersal process, as they consider species with unlimited dispersal ability; and still, with no restrictions in this regard the models predict local extinction for isolated populations in the mountains. The actual rate of extinction may be higher if the species cannot keep up with the accelerated CC due to limited capacity of migration; therefore, it is necessary to incorporate the potential for dispersal and life history in assessing the risk of extinction of the species.

In terms of justifying the use of howler monkeys as a research object for seed dispersal, some important information stands out. Although birds disperse a larger number of seeds, primates disperse the seeds of twice as many plant species as birds via endozoochory (Clark et al. 2001), and their ecological services are critical for recruitment of many medium and large seeded plant species (Amato and Estrada 2010). Howling monkeys are one of the largest neotropical primates, and they generally show the highest density among primate populations; also, the proportion of fruit in the howler diet goes from 10 to 60% (Julliot 1996) which makes them an important seed disperser. Howler monkeys are often the only large seed dispersal agents that may survive for a long time in small forest fragments and thus may play a crucial role in plant regeneration processes. Therefore, interactions between the primate species and the plant community are highly relevant to conservation purposes (Martins 2006).

6.4 Research Objectives

6.4.1 General Objective

Assess the capacity of seed dispersal by howler monkeys *Alouatta* genus and evaluate its potential as local and long-distance dispersers .

6.4.2 Specific Objectives

1. Design a model to simulate the dispersion of seeds of tree species by howler monkeys.

2. Compare different scenarios of abundance and distribution of reproductive trees and different seed sizes with respect to their Kernel, scattering frequency of events, maximum dispersal distances, and proportion of scats under latrines.

6.5   Research Questions

Specific Objective	Research Questions
1. Design a model to simulate seed dispersal of tree species by howler monkeys of the *Alouatta* genus.	What parameters are relevant as inputs for the design and operation of a seed dispersal model by howler monkeys *Alouatta* genus? Does the seed size influence digestion time in the monkeys gut?
2. Compare different scenarios of abundance and distribution of reproductive trees and different seed sizes with respect to their Kernel, scattering frequency of events, maximum dispersal distances, and proportion of scats under latrines.	What is LDD in the case of howler monkeys (*Alouatta sp.*)? Is there potential for LDD by howler monkeys? What ecological implications does seed dispersal by howler monkeys have on trees depending on their random or aggregated distributions and scarce or common abundances, and subject to different seed sizes?

7. THEORETICAL FRAMEWORK

7.1 Mechanisms and Seed Dispersal Modes

Dispersal is considered the movement of individuals from their source or location from where they were born and bred (in the case of plants), to another area where establishment and reproduction can take place. As vegetation is sessile , the dispersion of plant organisms in most cases is done by the transportation of seeds or other dispersion units; understood as the process in which seeds move away from the mother plant , commonly through a dispersing agent (Nathan et al. 2008). As the dispersal of plants is usually done through the seeds, it will be referred to as seed dispersal; however, dispersal may actually refer to structures called fruits or seeds involving diasporas (Vittoz and Engler 2007).

Dispersal mechanisms are essential to the natural distribution of the species and for the mobilization and exchange of genetic material in and out of stock (Howe and Smallwood 1982). Regarding the mechanisms acquired by plants to perform seed dispersal, it is considered that the morphology of both fruits and seeds can indicate the general form of dispersal (Howe and Smallwood 1982, Nathan et al. 2008). These strategies are based on different adaptations, from the nutritional value of a fruit to attract forgivers, floating body structures for moving through water, wing structures capable of air transportation, to mechanisms of release by tension

The classical way of classifying "syndromes" of dispersion is based on seed dispersal agents or vectors, usually by analysis of the morphology of the seeds. The main actors are biotic (animals and plants themselves) or abiotic (wind and water) and the respective syndromes or dispersal modes are called zoocory, autochory, anemochory, and hydrochory (Levin et al 2003). In some cases, within the same taxonomic family there may be different scattering mechanisms that may be adapted to be spread by birds, bats, rodents, water, wind, projectile action, or by gravity, such as Leguminosae and Lecytidaceae; suggesting that selective pressures on variables and fruits are clearly effective (Howe and Smallwood 1982).

According Cornelissen et al. (2003), dispersal modes have an impact on the paths, distance and places seeds can reach. This feature corresponds to a categorical classification, and can be sorted in descending order of importance: wind (**anemochory**) includes several types, very small dust-like hairs or trichomes at the end of the seed, or crushed with " wings "; **no help**, seed or fruit that fall passively on the ground, here it appears to be no outside help; **endocory**, transport through the digestive tract of an animal, usually a vertebrate (birds, mammals, reptiles). Usually happens with a luscious fruits of bright colors; **epizoocory** or **exocory**, external animal transport through adhesion mechanisms of seed to coat and feathers of animals, like hooks, barbs, or a sticky substance, also by animals that do not eat the seeds but eat the fruit pulp; by **accumulation behavior**, it happens in some rodents and birds that exhibit this behavior, burying seeds to protect food; by ants (**mirmecocory**), seeds have specialized appendices containing a nutritional value that makes them attractive to ants or associated insects; water (**hydrochory**), in this case are adapted to travel on the water

surface, by means of a hard tissue of low specific gravity; auto-release (**autochory**), occurs by throwing their seeds in explosive movements of their capsules; by **contraction**, seeds containing hygroscopic (moisture absorbing) tissue that promote the movement with different forms of moisture.

Physical modifications appear to be present to carry out a determined mechanism of dispersal, but they do not necessarily predict the actual process that occurs. Also, dispersal is scarcely mediated by a unique dispersing agent, and is not confined to the primary movement of the seeds of the tree to the ground, but rather involves subsequent movements that may be mediated by other agents, which is the case of **secondary dispersal** (Howe and Smallwood 1982, Ran and Muller -Landau 2000, Levin et al. 2003). Therefore, the generalized classification method that actually corresponds to a harsh initial approach and/or a hypothesis for dispersal mechanisms tend to lose or even misinterpret information and features of the process (Muller -Landau et al. 2003).

To explain this statement there are several examples, such as the fact that feathery seeds can be dispersed by wind as much as water; as a fruit adapted to be consumed by the extinct Pleistocene mega-fauna today is spread by rodents, and secondary dispersal may be through ants. It is important to understand that these "syndromes" of adaptation are useful only as an organizational tool, and are not a substitute identification of the actual study of the process by which dispersal is achieved (Howe and Smallwood 1982). This especially in the case of long-distance dispersal, where dispersal is weakly correlated with the mechanisms performed by mere morphology (Levin et al. 2003).

Another limitation of the traditional morphologic classification method is to find the relationship between dispersal syndromes and their effectiveness contribution for plants (their fitness). This is because the dispersal agents, even if they belong to functional groups different species with the same function) differ in efficiency, both quantitatively (quantities and distances of the seed dispersal) and qualitatively (treatment and seed deposition) (Levin et at . 2003 Schupp et al. 2010) . For more detail see chapter 7.4 and 7.5 .

7.2   Advantages of Dispersal for Plants

When considering the costs of the energy that plants invest in producing structures or modifications related to its dispersal mode, it is reasonable to think that there are advantages to being disseminated (Wenny 2001). In this context there are three, but it is important to keep in mind that they are not mutually exclusive, and may even be difficult to differentiate (Howe and Smallwood 1982, Wenny 2001).

7.2.1   Escape Hypothesis

Suggests that the most obvious advantage is the high mortality associated with the disadvantages of the proximity to the mother tree, and that density- dependent mortality of seeds or seedlings is explained by predation by rodents or insects, pathogen attacks , or competition between individuals germinated . However, this hypothesis – proposed by Janzen (1970) and Connell (1971)- although widely accepted , can be refuted with evidence

that mortality is random with respect to the density and distance from relatives, but in overall, there are studies that argue both, for and against this hypothesis (Howe and Smallwood 1982).

Long-distance dispersal studies, though crucially important for understanding the dynamics of plant populations, are difficult to implement (Levin et al. 2003), mainly for the same rarity of the occurrence of such events and the methodological challenge involving for dispersal patterns data collection. However, understanding these processes is essential to determine the genetic structure, expansion range, and other important characteristics of populations. Currently, there are genetic tools that have the potential for providing evidence of long-distance gene flow (only able to detect movement if it results in the successful establishment of individuals), and the use of chemical markers, or other distance measuring to track individual movement of seeds (Nathan and Muller -Landau 2000). (see also chapter 7.5).

7.2.2 Hypothesis of Colonization

This scenario applies to communities of successional species that accepts that habitats change over time, so the strategy of a mother tree would be to widely spread seeds so that they can find some favorable sites for germination and establishment (Howe and Smallwood 1982). It applies for species requiring the occurrence of disturbances to get clear openings, and thus their seedlings are able to establish, grow and reach their reproductive age. Thus mass production of propagules able to remain dormant or suppress growth until the increase of sunlight induces germination and/or accelerate the growth of seedlings is necessary. Thus, this strategy of spreading the seeds abundantly maximize the number of different sites occupied and increase the likelihood that some spaces are appropriate in the future (Wenny 2001).

By characterizing the morphological adaptations of diasporas for dispersal, and through the comparison of natural history, Howe and Smallwood (1982) note that generally small seeds with obvious morphological features for dispersal by wind are associated with colonization potential, while large seeds with corresponding reduced mobility are associated with greater competitive ability in saturated habitats, but it is clear that these statements are not strictly correct in all cases. In this context, small seeds are related to plants occupying temporary habitats so that they reproduce quickly, you are quickly replaced by other species, and adults rarely remain in one location for more than a couple of generations . This way of characterizing traits of the species groups resembles the study of plant functional diversity and its classification into functional groups, and although the authors do not express it this way, it is possible to relate the issues.

7.2.3 Hypothesis Directed Dispersion

Dispersal comprises directed nonrandom arrival and seed survival in predictable sites (Howe and Smallwood 1982). Venable and Brown (1993) explain that in order to benefit from this form of dispersal, a plant must submit fruit characteristics conducive to a dispersal mode over another, or must present a morphology that allows propagules to reach certain habitat patches often more specific than expected by mere chance .

However, Wenny (2001) argues that plants need not necessarily be specifically tailored to achieve targeted dispersion, or that this may occur in various situations in which a plant may have multiple dispersal agents, some of which can provide directed dispersal, and others colonization. Recent studies suggest that directed dispersal is more common than previously thought; also the importance of this form of differential deposition may be high if the subsequent seed predation, germination, growth and survival also depend on the site (Ran and Muller -Landau 2000).

7.3   Mutualism Paradigm

A large proportion of plants in most plant communities are dispersed by animals in tropical forests at least 50 to 75 % or more of tree species produce fleshy fruits adapted for animal consumption by birds and mammals (Howe and Smallwood 1982). In very humid tropical forests the proportion of tree species dispersed by wildlife can be 90%, and this will decrease as the climate becomes more seasonal. Thus, plants dispersed by wind will be more common in number and proportion in drier habitats (Howe and Smallwood 1982).

This way it's easier to understand the role that animals play as seed dispersers, maintaining the structure and composition of natural diversity, and the chain of events released by the disappearance of large-seed dispersers due to hunting or loss of habitat, and that the consequent reduction in pollination and seed dispersal represent a major threat to biodiversity. Therefore, it is easy to accept that the network of mutual connections in nature has important implications for species coexistence, the co-evolutionary process between them, and the resilience of ecosystems (Bascompte and Jordano 2007).

According to Wenny (2000), specialists plant species or tropical plants that produce high quality fruit (large fruit with one or two large pulp and seeds rich in lipids or proteins) attract frugivorous animals that provide a dispersal of high quality or effectiveness. Furthermore, generalist plants produce large quantities of fruit which in turn contain many small seeds and pulp which is mainly composed of sugars and water. Thus it is expected that opportunistic dispersal agents (or general) are less effective for dispersal because they are less dependent on fruits compared to specialists frugivorous (Wenny 2000, Schupp 2010). In other words one might expect that high quality fruit qualify for directed dispersal, and poor quality fruit colonization (Wenny 2001).

The implications of these observations led to think that the evolution of fruit and fruit-eating could be relatively specific, involving their respective co-adaptations. However, detailed studies in this regard have helped the understanding that coevolution between plants and their dispersers is not specific to species, but involves adaptation between large groups of plants and groups of dispersal agents (Wenny 2001), convergent evolution between functional groups of flora and fauna. However, it is important to consider that highly frugivorous animals are not necessarily better or more effective dispersers (see below) that the opportunistic frugivors, like animals that frequently visit the reproductive plants do not necessarily contribute the most to dispersal (Schupp et at. 2010) .

A very important aspect to consider is that seed dispersal only corresponds to a stage in the reproduction of plants, thus defining the quality of the dispersal is necessary to study not only dispersal patterns, but also the survival these seeds and seedlings. Thus, the effectiveness of dispersion or effective seed dispersal, can be defined as the probability that a dispersed seed survive to reproductive age (Schupp et al 2010). Such effectiveness is measured in terms of quantity (number of visits and ingested by visit number seeds) and quality (quality digestive site treatment and deposition) of dispersed seeds (Schupp et al. 2010).

According to Schupp (2010), there are animal seed dispersal agents associations that provide different values of quantity and quality of seed dispersal, these values vary and depend greatly on the foraging behavior, morphological characteristics of the dispersion, and their interactions with plant traits (as the size of the fruit and seed, seed numbers and presentation). Overall, Schupp (2010) discloses that although there are some dispersal agent assemblies more effective, various agents are important because they generate an additional dispersion among all, and their presence increases the resilience of the dispersion system , and the possibility DLD event (see also chapter 7.5).

An example of this is evident in the work of Jordan et al. (2007), which found that small passerine birds dispersed seeds over short distances (50 % dispersed at < 51m from the source) within covered microhabitats, and midsize mammals and birds dispersed long seed distances (50 % of mammals dispersed a> 495m, 50% of medium-sized birds at distances > 110m) mainly to open habitats; so dispersal distances and microhabitat of seed deposition are linked to the behavior of frugivorous vectors. Jordano et al. (2007) concluded that the frugivorous animals differ widely in their effects on gene flow of species, and that despite the various groupings of mutual frugivorous dispersers, it's likely that the events of long-distance dispersal devolved in a small subgroup of large animal species (see also chapter 7.5).

7.4   Spatial Patterns of Dispersal

Seed dispersal patterns reflect the set of all individual scattering events in a population (Levin et al. 2003). These are determined by the spatial patterns of reproductive adults, the number of seeds released and its corresponding seed rain, they also depend on the environmental characteristics and the dispersing agent (Nathan and Muller -Landau 2000). In this regard, Brooker et al. (2007) emphasizes that the initial spatial arrangement of species is critical in the process of dispersion, since the occupied space may limit the expansion of species ranges.

The seed production and outputs vary considerably between species and between individuals due to differences in fertility and mortality of seeds. Variations within populations are partially determined by the size of the plant location quality; that produces a direct impact on the availability of resources needed for reproduction, such as access to light, and the climatic variations that affect from year to year growth (Nathan and Muller -Landau 2000). Genetic structure and self- incompatibility systems may determine the degree of inbreeding and outbreeding depression, and thus the number and quality of seeds produced.

Additionally, the amount of seed aborted or predated before dispersal also vary between individuals and between years (Nathan and Muller -Landau 2000).

Patterns of seeds dispersed away from their source may be qualitatively different from patterns near their source because various processes are applied on different ranges and distances (Nathan and Muller -Landau 2000). In this regard, Takahashi and Kamitani (2004) found that the number and abundance of forest tree species decrease the greater the distance to natural forest at landscape-scale; similar to local scales, pattern distribution decreases as distance from the parent tree increases; meaning that distance is a limiting factor for dispersal. Nathan and Muller -Landau (2000) indicate that although it has been overlooked, secondary dispersal distances can increase seed dispersal.

The most widely used option to assess the final seed dispersal forms has been quantified through the arrival to the same habitats or microhabitats, also through modeling dispersal Kernels to estimate the distances of the dispersal distributions; however, none of these alternatives reflects the true heterogeneous spatial pattern of dispersal (Schupp et al. 2010). Seed deposition pattern accumulation shape curves and seed distribution abundances can help build theoretical models (Russo et al. 2006). Recently, spatially explicit models have been developed based on animal behavior, to investigate the heterogeneity of SD, the effect of the spatial structure of the parent tree in the quantity and patterns of SD, and the consequences of overlapping tree seed rain at the same time (Schupp et al. 2010) .

Spatial patterns of seed deposition are key in the chances of success in plant recruitment, because of the various effects of the processes occurring after dispersal (such as density- dependent survival and coexistence between species). These patterns also determine gene flow between populations over evolutionary time during the colonization of new habitats (Russo et al. 2006). However, it should be clear that although seedling recruitment depends on the arrival of seeds, the arrival of the same does not guarantee recruitment. We note the importance of understanding the process following the dispersion, ensuring the success of the sprouts, to understand the real importance of seed dispersal (effective dispersal) in the generation of spatial patterns and dynamics of plant populations (Nathan and Muller -Landau 2000, Schupp et al. 2010) .

7.5   Long Distance Seed Dispersal (LDD)

The distance over which plants disperse seeds depends on several functional traits as environmental conditions and time scale of the events (Vittoz and Engler 2007). The variability of the distance of seed dispersal can be represented by a curve of dispersal or scatter called Kernel, which shows the probability and rate of seeds reaching a certain distance from the source or tree stem; where the vast majority of seeds are dispersed short distances (Vittoz and Engler 2007, Nathan et al. 2008).

The Kernels "fat tail " illustrate a greater likelihood of long distance dispersal (LDD), although mostly at small scales, where the observations combine the contribution of different dispersal vectors and can't necessarily be extrapolated to longer distances (Nathan et al. 2008). The Kernel is a 2Dt distribution "fat tail" where LDD is more frequent than in a normal

distribution (Gaussian) or a negative exponential distribution with the same distance from the source. For a dispersal Kernel, fecundity determines the amount of scattering events that occur, and survival of the seeds after dispersal determines the fraction which corresponds to an effective dispersal (Nathan 2008 Schupp et al. 2010).

Recent studies have shown that "big steps" that disseminate through LDD have more influence than many "small steps" by local dispersion in the expansion of native species after the occurrence of changes in historical climate ranges (Nathan 2006). However, it is clear that most seeds move short distances (from zero to tens of meters, Howe and Smallwood 1982, Cain et al. 2000), so that these unusual LDD events are vital. For example, Nathan (2008) states that the probability of spread beyond 100 meters from the source is very low, although Cain et al. (2000) comments that maximum distances between 1 and 20km have been recorded for a large number of plant species.

LDD has been considered as "random" or a probabilistic dispersal (Nathan 2006). However, the precise definition of LDD may depend on the context of the study (ex. Beyond 100 m, Cain et al. 2000). Nathan (2006) clarifies that " two of the most common definitions of DLD are: 1) Absolute threshold distance that may be due to major physical and biological attributes (ex. 250m between patches); 2) relative threshold based on percentile of the tail of a dispersal Kernel (ex. 1% of all seeds dispersed to a distance of 500m average dispersal)."

A generalization accepted in LDD research is that the morphological adaptations of diasporas, which are typically used to identify the modes of dispersion by "standard" (specialized dispersal) dispersers determine local or "short" dispersal distances, and in turn, these mechanisms generally do not cause LDD. In addition, there are "non-standard" or generalist dispersers which do not seem to identify with any morphological adaptation, and can serve as primary or secondary dispersers (Howe and Smallwood 1982, Vittoz and Engler 2007, Nathan 2008, Nathan et al. 2006, Schupp et al. 2010).

In general , it is recognized that the above characterization is not exclusive, and can be concurrent processes for many plants because the reality is that a single species can be dispersed by multiple dispersal vectors (policory), including a vector traditionally considered efficient for LDD (wind, water, birds, bats, large mammals, Nathan 2008). However, we must recognize that the "non - standard" dispersal vectors have higher tendencies to attract LDD (Nathan et al. 2008). This is why the authors speculate that the "non-standard" vectors that generate fat-tailed Kernels dominate LDD events, although with a smaller proportion of dispersed seeds (Nathan et al. 2008). This is why studies should focus on general vectors and policory process, to better understand and predict the LDD.

Schupp et al. (2010) recognizes that although there are dispersal agents that are more efficient than other, there are advantages in considering the "merged seed rain" for the species, and the patterns of seed dispersal created by the joint efforts of all dispersal agents of a particular species. Thus, they will be vectors that disperse seeds locally (and in different microhabitats, critical for successful seedling establishment), and others that disperse over greater distances, increasing the chances of colonization of distant sites.

The joint action of various dispersal agents is extremely important for flora population expansion. Thus, it can be deduced that an increase in the number of scattering events, will in fact increase the number of LDD events. This in turn would lead to more frequent dispersal between subpopulations as the establishment of new subsets, so the more effective the dispersion at the local level, the greater the likelihood that the dispersion between metapopulations is effective (Schupp et al. 2010)

It is assumed that not only seed dispersal in general, but also the LDD can have adaptive value, and still be favored by natural selection. However, if the general vectors and extreme events that produce LDD are determined by chance regardless of the phenotype of the seeds, it is likely that morphological adaptations of diasporas are shaped by natural selection that benefits only local dispersal vectors, indirectly affecting the LDD (Nathan 2008).

A simple mechanistic model, as suggested by Nathan et al. (2008, fig. 2) is useful for evaluating the potential of a vector for LDD. This model describes three main stages in seed dispersal as long as it is carried out by one or more vectors: 1) **initiation** phase, where the vector removes the seeds of the plant, the main parameter is the load of seeds (Q) which depends on the fertility of the plant, phenology and its interaction with the behavior of the vector and the vector capacity; 2) the **transport** phase, where the seed vector moves away from the source, the main parameter is displacement velocity of the vector (V), which also depends on the directionality and intermittency; 3) the stage of **termination**, the main parameter is the passage time of the seeds through the digestive tract (P), which depends on both the seed traits, the vector and their interactions.
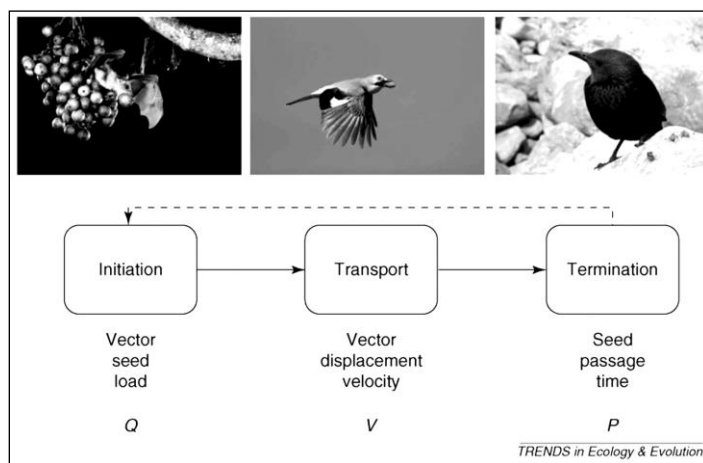
Fig. 2 Passive disperssl mechanistic model describing the three phases of dispersal, which in turn depend on three key parameters, Q, V and P. Extracted from Nathan et al. 2008

If the dispersal is channeled through various vectors, each phase will be repeated for each vector. In addition, each parameter noted above may be affected by environmental conditions, such as landscape structure and climate. LDD vectors may result if at least occasionally they exhibit high values of V and large values of P, or both, such vectors may contribute to the LDD although Q values are small (Table 1, Nathan et al 2008.). Several

authors emphasize that spread rates are higher in dispersed by wind, water and large animals (Vittoz and Engler 2007, Nathan 2008, Nathan et al., 2008) plants.

Table 1. Summary of the six most significant generalizations DLD mechanisms in plants. Extracted from Nathan et al. 2008.

Generalization number	LDD-promoting state or conditions	Relative effect on			Spatial scale of LDD events (log$_{10}$ meters)
		Vector seed load (Q)	Vector displacement velocity (V)	Seed passage time (P)	
G1	Open terrestrial landscapes	Low-intermediate	Intermediate	High	2–5
G2	Large animals	Intermediate-high	High	Intermediate-high	2–5
G3	Migratory animals	Intermediate-high	High	Low-intermediate	3–6
G4	Extreme meteorological events	Intermediate-high	High	Intermediate	3–6
G5	Ocean currents	High	Low-intermediate	High	3–6
G6	Human transportation	High	High	High	3–7

In this context, the howler monkeys (*Alouatta* spp.); mammals with a relatively large body size, locally common and widely distributed in most forest types (from low to 2500 m) are considered important seed dispersers for certain plant families, presenting an average of intestinal retention between 18-35 hours (Reid 2009, Arroyo- Rodríguez et al. forthcoming). Even though they are considered highly folivorous animals, 50 % of their diet is made up of fruits, and on the concept of effective dispersal (Schupp 2010) howler monkeys are potentially able to disperse large numbers of seeds, because of their size and their social habits that they move in family groups, and give a quality treatment in the gut to the seeds, producing disinhibition and scarification of the seeds; in addition to the above these monkeys have the ability to swallow large seeds (up to 4.6 cm long Arroyo- Rodríguez et al. forthcoming).

7.6   Models for Seed Dispersal

Few databases allow accurate characterization of the components of the seed dispersal curve over long distances, and many attempts to quantify the LDD are hampered by the fact that the adjustment process models are dominated by a large number of scattering events at close range, causing the tail of the curve to be poorly estimated. Another aspect that can introduce statistical problems is that the average and the tail distribution of the dispersion curve can vary independently (Cain et al. 2000) .

Obviously, LDD is difficult to measure empirically (Cain et al. 2000, Clark et al. 2003, Russo et al. 2006, Nathan 2008, Nathan et al. 2008, Will and Tackenberg 2008, Schupp 2010), so models have been used to measure such process. "Over recent years, models have been developed that focus on the role of LDD in metapopulation dynamics, Holocene migrations, genetic differentiation of populations, biological invasions, global warming, habitat fragmentation and competitive co-existence" (Cain et al. 2000).

According to Cain et al. 2000, models incorporating LDD describe it as a layered process, generating two behaviors of movement: one that simulates the local dispersion events (a short distance), and one for LDD events (because the seeds are scattered by more than one mechanism). Many studies have characterized the processes of dispersal layered with mixed models, where different probability distributions are used to model both cases.

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Likewise, Will and Tackenberg (2008) explained that classical diffusion models have shown limitations that understate LDD events, like the mixed model with thicker lines, that although they predict LDD, they do not contemplate the fact that seed dispersal through wildlife cannot be modeled as a decreasing function of distance, in addition, require the inclusion of habitat preferences, behavior and movement patterns.

Spatially explicit models represent a promising tool for the study of LDD, and their use has had much progress in understanding wind dispersal (dispersal mechanism best studied so far) because they simulate their dispersal curves more realistically. On the other hand, zoocory is closely influenced by a variety of both animal and floral traits, and there have been few attempts to model seed dispersal by animals (Will and Tackenberg 2008). According to Russo et al. (2006) and Will and Tackenberg (2008), most studies based on mechanistic models of dispersal by animals predict dispersal curves based on gut retention time and seed displacement rates, but until recently spatially explicit motion directionality information is being incorporated.

Also, the existing knowledge in animal behavior and characteristics of plant species should be combined to predict seed dispersal by fauna, but this behavior is very complex and even less understood that the behavior of the wind, because they are influenced by conditions of abundance, the characteristics of alternative foods, competition with other plant species, predation, individual behavior of the dispersion (gender, age, hierarchy) and social systems (Nathan and Muller -Landau 2000 , Russo et at . 2006). Will and Tackenberg (2008) argue that the inclusion of information on the behavior of dispersal agent is indispensable for conducting realistic descriptions of seed rain , so a compilation of home ranges of other large animals could improve predictions as to the spatial extent of the dispersal of seeds . Russo et al. (2006) suggests to also incorporate the size of the agent's body, home range and social system.

It has been shown that spatially explicit models incorporating realistic kernels can elucidate ecological and evolutionary dynamics. They are superior in terms of explanatory power with respect to the dispersal models treated simplistically (Nathan 2008). Another point that the author encloses, is that studies should be integrated with scattering investigations affecting post-dispersal population size, survival and successful establishment of species factors.

In conclusion, it has become clear that the success or failure of seed dispersal depends much more on changes in vectors, with comparable small range in intraspecific traits of species (Soons et al. 2004, Will and Tackenberg 2008). In addition, greater efforts should be directed to quantify LDD events, as if the aim of the study is to predict the possible outcomes of fragmentation, climate change and other aspects of global change, considering collecting data pertaining to specific dispersal curves (Cain et al. 2000).

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9. RESEARCH ARTICLE:

Parameterization, Development and Ecological Implications of a Seed Dispersal Model by Howler Monkeys

Rivera-Bialas, Rebecca; Vilchez, Sergio; Finegan, Bryan; Imbach, Pablo.

ABSTRACT: Seed dispersal distance values represent key information that should be incorporated to climate change species distribution modeling; however, this information is very difficult to obtain empirically. Howler monkeys are important and effective seed dispersers of tropical forests, but still much debate exists regarding their ability to produce long-distance seed dispersal events, and concerning their clustered patterns of seed depositions in latrines. Mechanistic models of seed dispersal that include theoretical concepts, empirical data and animal behavior and movement assumptions, can help address particular hypotheses and predict outcomes to help understand the role of howler monkeys for different scenarios of canopy tree species abundance, spatial distribution and seed sizes. Thus, we created a model based on parameters obtained from literature review and field observations, and our results suggest that distances of seed dispersal can be reached up to 550m from parental trees, and although LDD events may occur of up to 3 km, howler monkeys contribute mostly to local seed dispersal. Food availability modelled by fruiting tree abundance has an effect on seed dispersal distances and number of seed dispersal events; as clustered aggregations of reproductive trees also have an effect on seed deposition patterns. Defecations in non-latrine sites led to significant longest seed dispersal distances, and the model suggests seed size to have an effect on the proportion of seeds not defecated under latrines. Howler monkeys are important seed dispersers and even though their dispersal abilities have limitations, their contribution to forest structure, its regeneration and the regional survival of some trees species has been proven more than once. Our *MonkeySeed* model is a promising tool for the study and comprehension of seed dispersal distances through endozoochory, and whose results can be applied in further studies of canopy tree migration and species distributions throughout climate change scenarios.

Key words: howler monkeys, seed dispersal model, latrines, long-distance dispersal, seed deposition patterns, dispersal events

INTRODUCTION

It has become very clear in recent years that there cannot be an understanding of plant populations and community dynamics without an adequate comprehension of how seed dispersal works (Nathan & Muller-Landau 2000, Muller-Landau et al. 2008, Wang & Smith 2002). This statement is especially important in tropical rain forests, where the great majority of tree species -up to 90% of canopy species- have fruits adapted for consumption and seed dispersal by frugivorous vertebrates (Howe and Smallwood 1982, Howe 1993, Nasi et al. 2002). As it is, most frugivorous species that act as dispersal agents have their own feeding behavior, digestive rhythms, movement patterns, and ways of handling fruit; therefore affecting spatial patterns of seed deposition, seed viability, seed post-dispersal processes (Schupp 1995, Andersen 2002, Muller-Landau et al. 2008, Bravo 2012), and overall dispersal effectiveness (Schupp 1993, Shupp 2010).

Since seed dispersal effectiveness depends on the quantity and "quality" of seed dispersal (Schupp 1993); many authors have come to the realization that howler monkeys (*Allouata sp.*) represent an important, widespread, and effective seed disperser depending on the plant species and region (Andersen 2002, Martins 2006, Amato & Estrada 2010, Anzures-Dadda et al. 2011, Bravo 2012). This statement is based on the fact that these primates are distributed in the majority of tropical forest of America (from low lands to 2500m; Reid 2009),

they generally show the highest density among primate populations, and are one of the largest neotropical monkeys (Julliot 1996), which gives them the ability to disperse a high number of medium to large-seeded plant species through endozoochory (Amato & Estrada 2010); furthermore, as they travel and eat in groups because of their social behavior, they can potentially disperse greater quantities of seeds. Another very important fact to consider is their long digestive time periods (Yumoto et al. 1999, Andersen 2002), which ideally allows them to travel further and disperse seeds farther from parent trees than other frugivores, also excreting a large number of viable seeds (Chapman 1989).

In contrast, it has also been argued that *Allouata* species can be low quality dispersers because of their long inactivity times (Pavelka & Knopff 2004) and aggregated defecation patterns that greatly affect post dispersal seed fate (Andresen 2002, Bravo 2012). In the case of howler monkeys, their cohesive social groups that defecate together, mostly under sleeping sites or latrines (Julliot 1996, Andresen 1999), could represent a disadvantage for the establishment of seed/seedlings due to density-dependent mortality issues (Howe 1993, Andresen 2002, Bravo 2012). However, single individuals can excrete at different times and places than the rest of the group, integrating a scattered component into the configuration of their seed dispersal (Bravo 2009) that could be based on "in-transit site" defecations (Russo et al. 2006) when moving from site to site. This scatter component though potentially relevant has not yet been measured, and it is unknown how often and in what context it is occurring (Bravo 2009). Also, some authors claim advantages to howler monkeys clumped defecation patterns and its associated secondary dispersal fate (see also Chapman 1989, Estrada y Coates-Estrada 1991, Estrada et al. 1993, Julliot 1997, Andersen 1999, Andersen 2001, Pouvelle et al. 2009).

Nevertheless, a big discussion exists regarding whether if howler monkeys are capable to disperse seeds long distances, or do they mostly contribute to seed deposition under latrines and local dispersal.   In recent years it has become more and more evident that the study and understanding of long distance dispersal (LDD) represents an important part of the puzzle for the comprehension of plant population dynamics and structure, their movement and colonization across continuous and fragmented landscapes (Nathan 2006, Nathan et al. 2008, Levey et al. 2008, Schupp et al. 2010), and how organisms disperse and eventually migrate, to help predict in what way species adapt and persist in time and space with climate change (Cain et al. 2000, Knowlton y Graham 2010). In this sense, howler monkeys may represent a promising LDD agent, as many authors believe that when it comes to animal-dispersed seed, LDD events may rely on a small subset of large mammal species as efficient dispersal vectors (Jordano et al. 2007, Vittoz and Engler 2007, Nathan et al. 2008, Schupp 2010).

LDD studies, though crucially important for large-scale dynamics of plant communities, are difficult to implement and measure empirically (Cain et al. 2000, Clark et al. 2003, Levin et al. 2003, Russo et al. 2006, Nathan 2008, Nathan et al. 2008, Will and Tackenberg 2008, Schupp 2010). That is why this aspect of research has depended more on the use of mathematical simulation models that help predict outcomes for seed dispersal, because models require more assumptions than empirical data and therefore are easily applied (Levey et al. 2008); however, few of these studies have embraced this approach using endozoochory as a means for dispersal because of its great conceptual complexity (Russo et al. 2006, Will & Tackenberg 2008, Cousens et al. 2010, Correa-Cortes and Uriarte 2012).

In this regard, inclusion in a model of information on the behavior and movement of the dispersal agent is essential for conducting realistic simulations of seed dispersal patterns (Will and Tackenberg 2008, Correa-Cortes and Uriarte 2012). Correspondingly, it is also important to include factors that may influence the spatial distribution of seed pattern deposition, like abundance and aggregation of adult trees (Correa-Cortes and Uriarte 2012), as well as seed or fruit traits (Clark et al. 2005). This is because even in plant species with the same dispersal syndromes, variation in fruit and seed characteristics may have an additional effect on their seed dispersal patterns (Muller-Landau et al. 2008).

In synthesis, the objective of this study is to contribute to the building of knowledge of seed dispersal by howler monkeys in different scenarios of reproductive tree abundance, spatial distribution, and seed size. We constructed a simulation model that incorporates howler monkey's behavior, feeding habits, seed retention time, and real movement data in order to simulate seed dispersal distances and seed dispersal patterns. We expect to better understand the concept of (and quantify) LDD for howler monkeys, measure its scattered component, and translate this information into its ecological significance for the resilience of different tree species and their ability to migrate and keep pace with changing climates and other aspects of global change. These results will allow us to better understand the underlying importance of the howler monkey in their still debated contributions to seed shadows, and the never-ending ecological intricacy of forest community dynamics.

Study site

The Barbilla National Park (Fig.3 B) is located in the provinces of Limon and Cartago in Costa Rica, covering an area of 11,994.74 hectares, between 200 and 1600m. Its main objective is to provide protection to a large area of tropical rainforest in pristine condition, containing great diversity of flora and fauna, and many endangered species. It is also an area that has a high water production of vital interest for the supply of drinking water to neighboring communities, and has great historical value to be found in surrounding areas populated in great part by the Cabecar indigenous group (SINAC 2012).

The study area is the lowest part of an altitudinal gradient known as *Caribe-Villa Mills* (Fig.3A) that is located on the Atlantic slope of the Talamanca Cordillera, with an elevation range of approximately 300 to 2800m (SINAC 2012). The altitudinal gradient has an area of 227,674 hectares, and belongs to the regime of precipitation and climatic region Caribbean Southern Caribbean (IMN 2009).
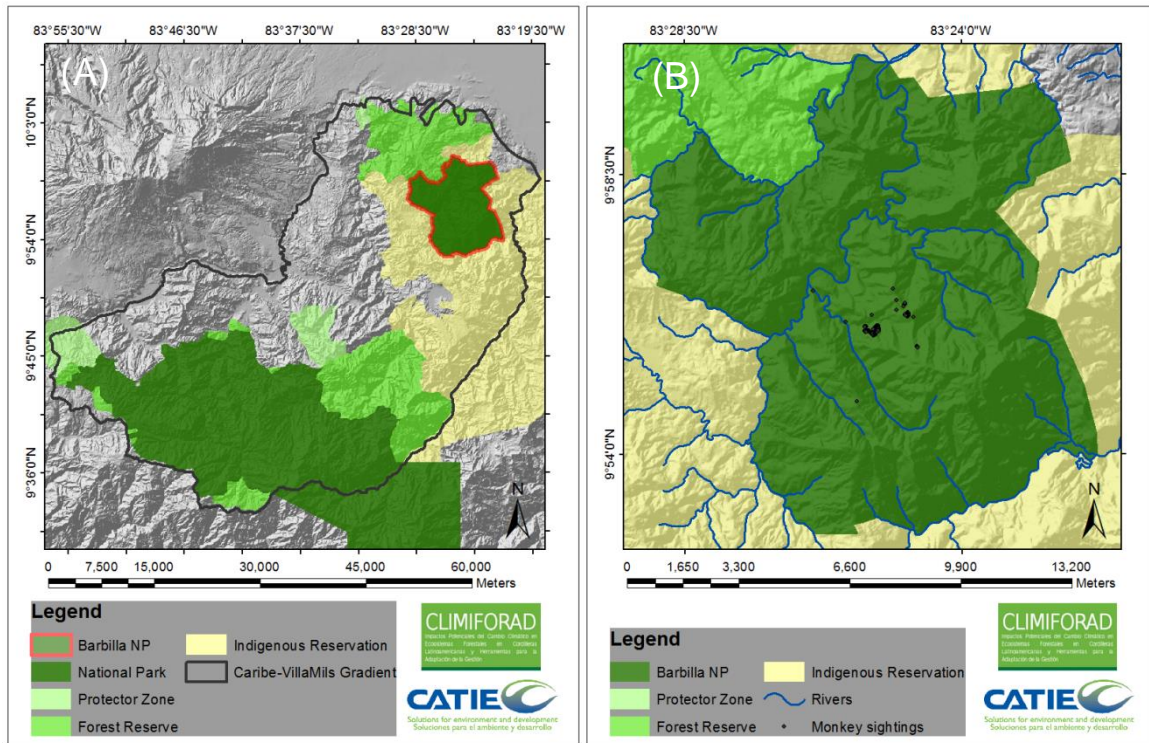
Fig. 3. Study site. (A) Caribe-Villa Mils altitudinal gradient, (B) close up to Barbilla National Park.

METHODS

To build the seed dispersal curve obtained by howler monkeys (*A. palliata*) we designed a rule-based stochastic model that simulates the movement of the animals through an actual or fictional landscape. Movement parameters of the monkeys were acquired in the field, for which we estimated home range, speed, distance and angle of locomotion from one tree to another. We also observed the monkeys activities patterns during day time. The amount of time the dispersal agents invest in their daily activities, and gut retention times (GRT) for different seed sizes, were obtained by literature review.

We also simulated six fruit tree abundance and distribution scenarios, as well as three seed size-GRT scenarios to inquire for the most sensitive parameter in the model and its ecological implications for different tree species that can resemble the conditions we have replicated.

Parameters obtained in the field

A troop of *A. palliata* and some solitary males were followed for 90 hours spread between March and July 2013. Daily observation periods were ideally 10 continuous hours. The spatial location of feeding trees and resting sites, along with their travel routes were tracked with a Garmin GPS with ± nine to eleven meters of accuracy. It should be noted that the feeding activity that was recorded only includes trees (leaves, fruits and flowers).

For speed, angles, and distances traveled by howler monkeys, we used the spatial analysis tool Geospatial Modelling Environment, GME, version 0.7.2.0 (Beyer 2012). GPS points were used to extract travel movement angles and speed of the monkeys from one point to the other (Figure 4). These values will be extracted randomly by the model whenever needed.
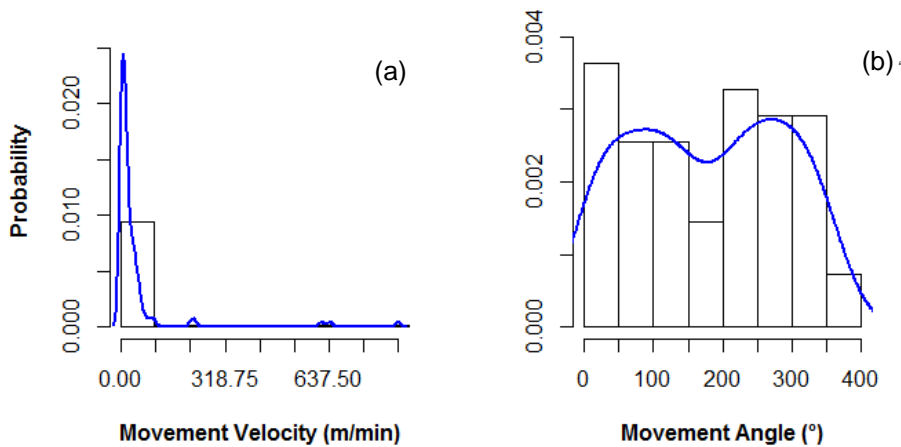
Fig. 4. Probability density associated with movement speed and angles of *A. palliate*; data obtained in the field, at Barbilla National Park, Siquirres, Costa Rica, March-July 2013.

Parameters extracted from literature

Based on literature review, information on how *Alouatta sp.* individuals spend time on their daily activities (feeding, resting, traveling, and gut retention time) was collected (see Appendix 1). The available data was standardized by the number of minutes per day that the monkeys spent on each activity for each study, and the frequency of occurrence of each activity during the day (two times a day for each activity); then by using bootstrapping we generated a vector of 250 values for every parameter to better predict the probability distribution of the time howler monkeys spend on each activity during the day time (fig. 5).
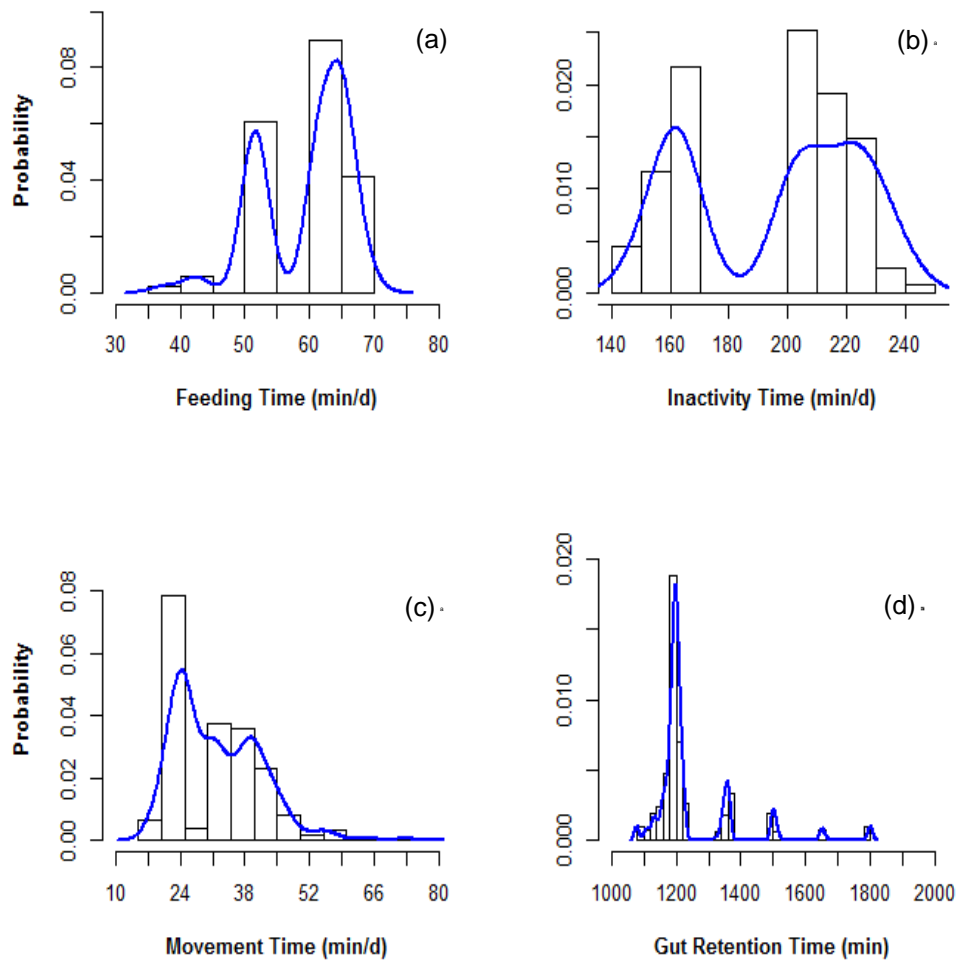
Fig. 5. Probability density associated with daily activities of *A. palliata*, according to literature.

Simulation Model

We designed a rule-based stochastic model called *MonkeySeed* programmed with the R version 2.15.2 package (R Development Core Team 2011) that simulates seed dispersal by howler monkeys (fig. 6, Appendix 5); it works on the foundation of the parameters indicated in Table 2. This model simulates spatial patterns and distances of seeds dispersed in a landscape with a single dispersing agent, and constructs the respective dispersal Kernels. In this case, it has been parameterized for the howler monkey genus *Alouatta*, but it could be used for other mammals if the necessary information is available.

Table 2. Summary information on parameters used for the model *MonkeySeed*

Parameter	Description	Value	Source
XYini	Potentially initial point simulation coordinates	(x, y)	Random points obtained according to the biggest diameter of home ranges from literature (Chapman 1988).
Vtray	Movement speed	0.022-14.062 m/min (fig.2a)	Estimated from field data.
Atray	Movement angles	1.22-353.64° (fig.2b)	Values obtained in the field.
Tmov	Travel movement time	9-98.67 min/d (fig.3c)	Bernstein 1964, Mittermeier 1973, Braza et al. 1981, Garcia 1993, Andersen 1999, Estrada et al. 1999, Bravo & Sallenave 2003, Pavelka & Knopff 2004, Garber & Jelinek 2006, Dunn et al. 2009
Tfeed	Feeding time	34.71-85.02 min/d (fig.3a)	Bernstein 1964, Mittermeier 1973, Braza et al. 1981, Garcia 1993, Andersen 1999, Estrada et al. 1999, Yumoto et al. 1999, Bravo & Sallenave 2003, Pavelka & Knopff 2004, Garber & Jelinek 2006, Dunn et al. 2009
Trest	Resting or inactivity time	63.96-283.53 min/d (fig.3b)	Bernstein 1964, Mittermeier 1973, Braza et al. 1981, Garcia 1993, Andersen 1999, Estrada et al. 1999, Bravo & Sallenave 2003, Pinto et al. 2003, Pavelka & Knopff 2004, Garber & Jelinek 2006, Dunn et al. 2009
Tdig	Gut retention time (GRT)	960-2100 min (fig.3d)	Estrada & Coates-Estrada 1984, Estrada & Coates-Estrada 1991, Julliot 1996, Pruetz et al. 1996, Yumoto et al. 1999, Serio-Silva & Rico-Gray 2002, Stevenson et al. 2002, Wehncke et al. 2004, Martins 2006
XYseed	Coordinates for possible feeding trees, with seeds for dispersion.	(x, y)	20x20m grid scenarios generated for 6 distribution and abundance types of seeded trees in the landscape.
Tsimul	Simulation period of time (days, months, years)	2 months	Chosen depending on the phenology of the tree species of interest.
It	Iterations (simulations)	10000	According to specialist criteria a minimum of ten thousand simulations is recommended.
Radio	Search radius for trees with fruits	20 m	Chosen as the minimum space between trees.
Tday	Day time	13 h	Value generated from literature review (Mittermeier 1973, Garcia 1993, Stoner 1996, Estrada et al. 1999, Bravo and Sallenave 2003) and field observations.
Tnight	Night time	11 h	Value generated from literature review (Mittermeier 1973, Garcia 1993, Stoner 1996, Estrada et al. 1999, Bravo and Sallenave 2003) and field observations.

In the case of this study, the models outputs are the result of ten thousand simulations, each one of a period of two months' time (Table 2). In every iteration, the model simulates the path and activities of a single *Alouatta* individual, maintaining a sequential order in their daily actions (movement - feeding - resting); starting in the early hours of the morning until the end of the day (fig. 6 and 7), for a simulation period of time that the user can determine, and may be based on the phenology of tree species analyzed. Time probability values for each activity are chosen randomly based on a vector of values that come from the literature review (fig. 5 a, b and c). The number of times that monkeys exercise each activity is based on field observations; they move, eat and rest twice daily as a group; this

assumption was corroborated with secondary information (Mittermeier 1973, Garcia 1993, Stoner 1996, Estrada et al. 1999).
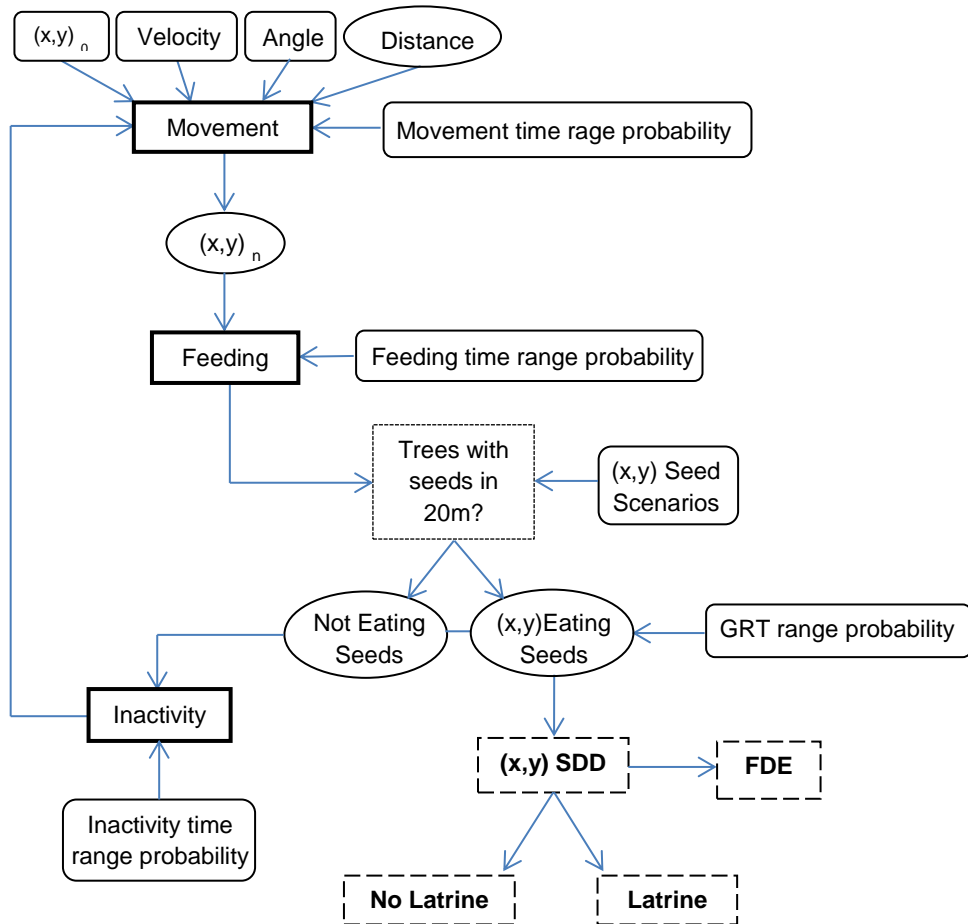
Fig. 6. Flow diagram of the simulation model of seed dispersal by howler monkeys (*Alouatta sp.*). Rounded boxes represent model inputs, squared boxes exemplify daily activities the monkeys perform, circles are calculations that the model executes but does not store in its memory, the short-dashed box is a question the model must answer, and long-dashed boxes are model outputs. GRT=gut retention time, SDD= seed dispersal distance, FDE= frequency of dispersal events.

The initial position of the monkey in the landscape (a quadrant of 22 575 ha over our study site) is chosen randomly from a vector of georeferenced points that are spaced evenly according to the largest diameter for the home ranges (1173m assuming a circular shape for those home ranges) obtained from literature (Estrada 1984, Estrada and Coates -Estrada 1984, Chapman 1988; Julliot 1996, Stoner 1996, Serio-Silva and Rico-Gray 2002, Bravo and Sallenave 2003, Pinto et al 2003, Gavazzi et al 2008, Dunn et al. 2009, Amato and Estrada 2010). Also, we assumed the simulation period to start at the first sun light hour of the day (6am), but the user can decide to have the model start the simulations randomly in time.

To start a simulation, a virtual path is estimated based on an initial position, the angle and speed of travel. In turn, the distances between each of the monkey's movements depend on time and speed parameters.

$$X_{(t+1)} = X_{inicial} + Cos(angle) + Distance$$
$$Y_{(t+1)} = Y_{inicial} + Sin(angle) + Distance$$

Where the distance is estimated:
$$Distance = Speed\ X\ Travel\ movement\ time$$

All these parameters are taken randomly from different data vectors (fig. 4 and fig. 5c) to estimate the next position. Given the random distribution of our movement angle values (fig. 5d), the direction of the movement that is simulated is basically a random walk.
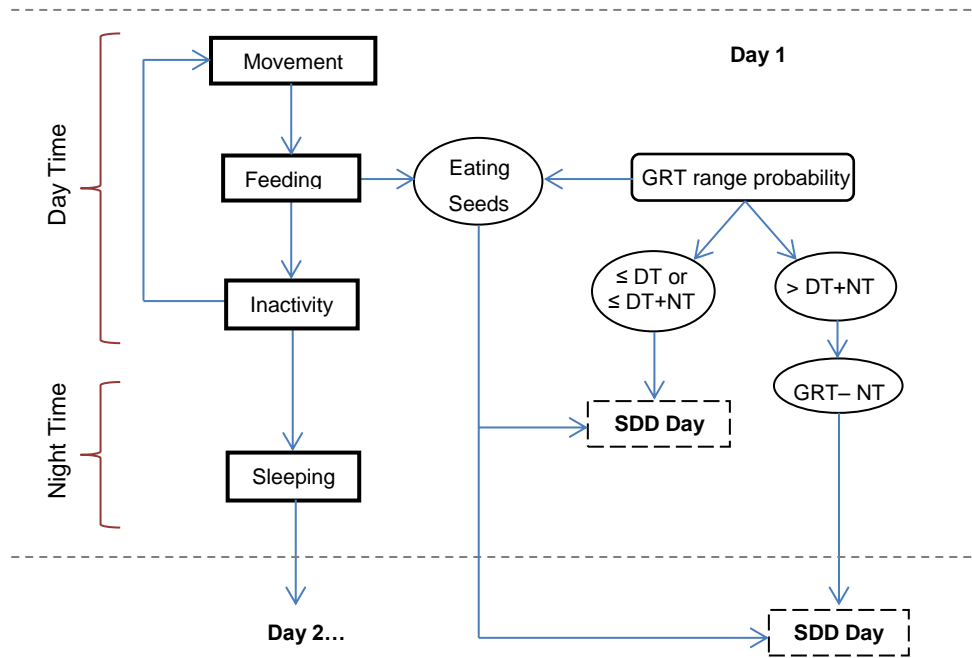
Fig. 7. Summary of Gut Retention Time breakdown between Day Time and Night simulations. Rounded boxes represent model inputs, squared boxes exemplify daily activities the monkeys perform, circles are calculations that the model executes but does not store in its memory, and dashed boxes are model outputs. GRT=gut retention time, DT= day time, NT= night time, SDD= seed dispersal distance.

The simulated monkey will move in the landscape calculating its path (based on a grid of points distributed equally every 20 meters) until its feeding time at any given point. At that time the model will search in a 20m radius for fruiting trees (our minimum distance between trees), if a fruit tree is not found, the model concludes that the monkey ate leaves; but, if a fruit tree is encountered, the model will start counting a gut retention time (GRT) drawn randomly from a simulated vector of possibilities obtained from literature (fig. 5d). GRT can therefore start in one simulation day and end the next (fig. 7); depending on its duration, and the monkeys movement patterns; this will influence if seeds are dropped in latrines or not.

Fruiting tree distribution and abundance scenarios

The effect of fruit tree distribution and abundance in the landscape was evaluated for seed dispersal. For each type of distribution, random and aggregated, we ran the following categories for abundance: one tree every ten hectares (called Rand1 and Clust1), one tree per hectare (Rand2 and Clust2), and ten trees per hectare (Rand3 and Clust3). These scenarios were based on actual point coordinates extracted randomly from a 20 meter grid of points from the study site, with the use of GIS tools like ArcMap 10.1 and Geospatial Modelling Environment, GME, 0.7.2.0 (Beyer 2012).

Seed size-GRT scenarios

In regards to gut retention time (GRT), some authors believe that seed size is relevant to digestion time: the bigger the seed, the longer the time it takes to be excreted by the monkey (Julliot 1996). With this in mind, we took values of seed size (seed length) and GRT that have been published by Julliot (1996) and Yumoto et al. (1999) and demonstrated a linear effect between the two variables (fig. 8).
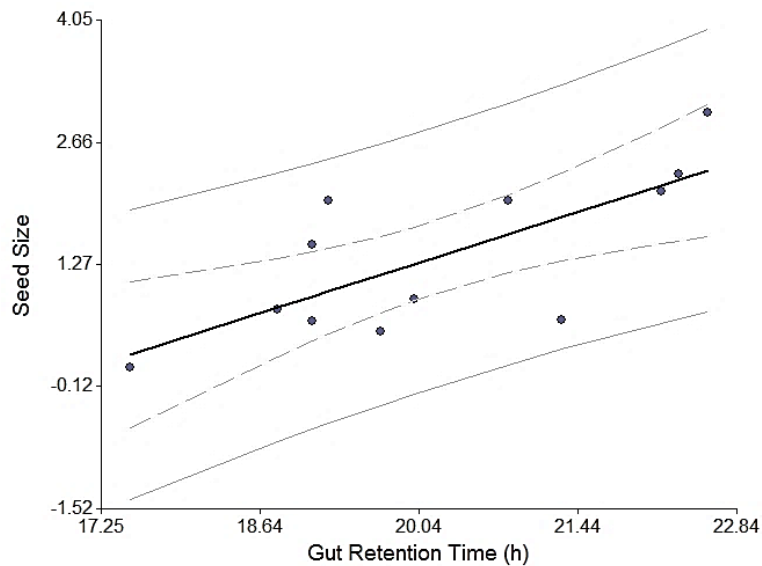
Fig. 8. Linear regression (R^2=0.54, p=0.006) estimated for seed sizes and gut retention times published by Julliot (1996) and Yumoto et al. (1999). Solid gray lines represent prediction bands, and dashed gray lines represent confidence bands.

The equation of the regression is:

$$Seed\ Size = -6.98 + [0.41\left(\frac{GRT}{60}\right)]$$

We then created a range of values of seed sizes based on published information by Julliot (1996) and Yumoto et al. (1999) of seed size and GRT by using bootstrapping to create 250 replicates of the values, and then, with the use of a cluster analysis we generated three different groups or scenarios of GRT for the model according to seed sizes (Table 3).

Table 3. Seed size (cm) and gut retention time (GRT) groups created with a cluster analysis.

Group	n	Mean	SD	Min	Max	GRT (h)
Small Seed (0.40-1.38cm)	205	1.14	0.19	0.4	1.38	18-20
Medium Seed (2.18-2.33cm)	26	2.29	0.05	2.18	2.33	22-23
Large Seed (3.27-5.32cm)	19	3.83	0.78	3.27	5.32	25-30

Model outputs

Model outputs are stored as R files (extension ".RData"; R Development Core Team 2011), where all data can be reached. In these images 4 lists are stored: the first list is a summary of total simulations with latrine and non-latrine frequency of dispersal events, mean, 1st and 3rd percentile, and minimum and maximum values of seed dispersal distances; the second list contains 10 thousand lists (one for every model iteration): coordinates (x, y) of seed deposition, distances of seed dispersal and a frequency record of latrine and non-latrine events; the third list is one of the total distances recorded for distribution amplitudes; and the last list holds the record for all frequencies of seed dispersal events for every iteration simulated.

Data Analysis

Seed dispersal kernels (frequency distributions of dispersal distances) were constructed with "*density*" and "*kernel*" functions with the R package version 2.15.2 (R Development Core Team 2011), for the sum of all simulation cycles for every scenario of the study; adjusting the nonparametric function with the amount of dispersal events in response to dispersal distances. Based on this model, the density function of a Gaussian Kernel 1D was adjusted.

We used various components of the seed dispersal curve to characterize seed dispersal distance: mean, minimum, maximum, and 50th and 99th percentiles of the total dispersal curves for each simulated scenario. LDD events were defined as those larger than the 99th percentile values of total simulations for each scenario, and frequency of LDD and all dispersal events in general were evaluated in a qualitative manner.

Spatial distributions of seed dispersal for one of the ten thousand simulations for every scenario (that represents the 99th percentile of maximum distances) were constructed with the use of the library "*spatstat*" (Baddeley and Turner 2005) with the R package version 2.15.2 (R Development Core Team 2011); the "*K*" function was also used to characterize spatial clustering or regularity of seed depositions; and with the use of the "*distmap*" function, other information used as metrics to categorize differences between scenario spatial patterns of seed deposition, like the mean distances between centroid of seed deposition clusters. Also, the minimum convex polygon method was used to recreate hypothetical home ranges for the simulated monkeys, again using ArcMap 10.1 and Geospatial Modelling Environment, GME, 0.7.2.0 (Beyer 2012); additionally, an analysis of variance (ANOVA) with range transformation on the Euclidean distances of the same spatial patterns of seed dispersal was performed for all scenarios to find differences within scenarios.

With the use of the "*splacs*" library (Rowlingson and Diggle 2013), in the R package version 2.15.2 (R Development Core Team 2011), home range (minimum convex polygons) areas were estimated, with "*chull*" function, for total iterations and all scenarios simulated that

presented more than six dispersal events. This data was then used to calculate linear regressions with the use of "*lm*" function, between home range and maximum dispersal distance *log* values.

Finally, an Independent t test was run to compare latrine and non-latrine dispersal distances for all nine scenarios. Percentages of latrine and non-latrine deposition occurrences were also used to compare qualitatively between different scenarios of seed dispersal by howler monkeys.

RESULTS

Seed Dispersal Distance, Distribution and Frequency

All howler monkey seed dispersal curves were long-tailed, highly leptokurtic and biased toward local-scale dispersal (dispersal distances between 50 and 100 m; Table 4; fig. 9); also, some multimodality can be noted by examining dispersal kernels for every individual simulation (fig. 10 and 11). Seed dispersal could reach very long distances (up to 2421m for abundance and distribution scenarios, and 3094m for seed size scenarios), even though the totality of the dispersal curves had 99% percentiles that did not rise above 555m or 619m (for abundance and distribution scenarios, and seed-size scenarios respectively; Table 4); also, given that the threshold for LDD is the 99th percentile, only 1% of the estimated dispersal curves presented LDD events for every scenario as seen in Table 4. Mean dispersal distances, 50th and 99th percentiles are displayed in Table 4 for every scenario simulated.
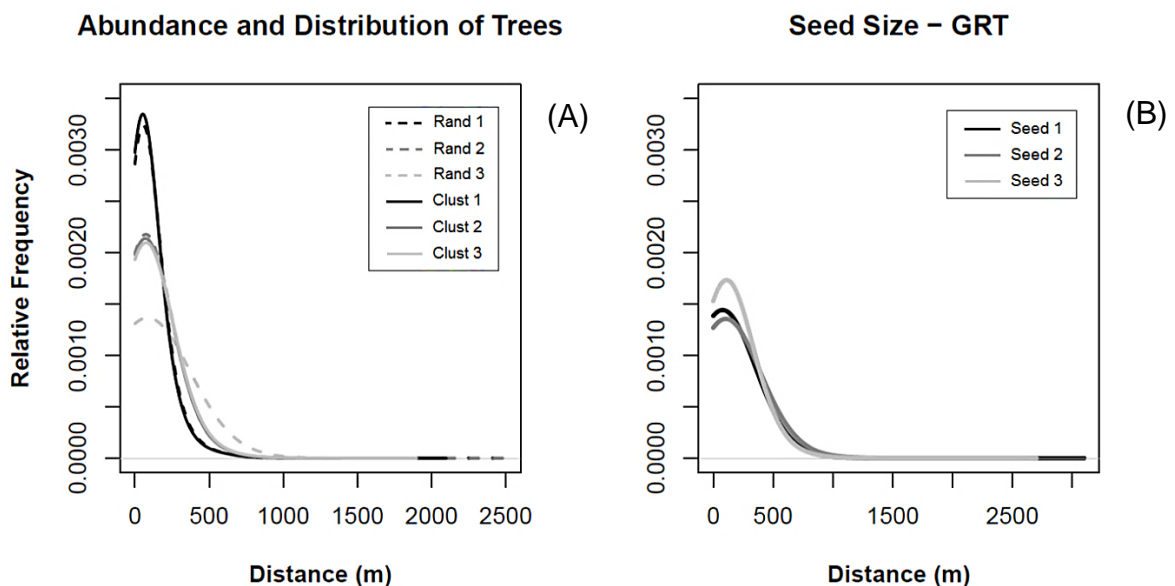
Fig. 9. Seed dispersal distance frequency distributions of the sum of all 10000 iterations simulated for every scenario studied. (A) Scenarios Rand 1, 2, 3, and Clust 1, 2 and 3 symbolize random distributions of ten trees per ha, one tree per ha, and one tree every ten ha, and clustered distributions of ten trees per ha, one tree per ha, and one tree every ten ha respectively. (B) Scenarios Seed 1, 2 and 3 signify Small Seed (0.40-1.38cm), Medium Seed (2.18-2.33cm), and Larger Seed (3.27-5.32cm) respectively.

Table 4. Summary of seed dispersal distances (in meters) for every simulated scenario of seed dispersal by howler monkeys. Frequency of seed dispersal occurrence, mean dispersal distance, standard deviation, 50th and 99th percentiles, maximum distance of dispersal recorded, frequency of LDD events (larger than 99th percentile), and percentage of LDD events.

Scenario	n	Mean	SD	Min	Max	P(50)	P(99)	> P(99)
Random, ten trees per ha	398110	88.08	105.74	0.00	2421.70	48.61	530.11	398
Random, one tree per ha	97030	96.27	109.50	0.10	2380.62	57.07	537.68	97(
Random, one tree every ten ha	11446	97.87	109.26	0.56	1810.15	58.04	534.78	11-
Cluster, ten trees per ha	232240	85.14	103.94	0.04	2087.84	45.87	526.98	232
Cluster, one tree per ha	74325	92.72	108.07	0.02	1371.67	53.07	541.74	74-
Cluster, one tree every ten ha	12252	97.23	111.91	0.26	1881.30	57.42	554.96	12:
Small Seed (0.40-1.38cm)	100614	89.66	104.37	0.13	3094.18	51.77	524.54	100(
Medium Seed (2.18-2.33cm)	88126	122.92	130.03	0.17	2396.46	80.21	618.81	88:
Large Seed (3.27-5.32cm)	82363	134.58	128.29	0.11	2650.49	95.30	618.87	82:

In regards to tree abundance and distribution scenarios, it is clear that scenarios with greater potential for longer seed dispersal distances are those with the most reproductive trees (ten and one tree per ha); less availability of fruiting trees affects not only the probability of LDD but the number of dispersal events occurring in each simulation (fig.10; Tables 4, 5). Also, the number of dispersal events per simulation varies greatly between these six scenarios; there is greater asymmetry of dispersal events in clustered distribution of fruiting tree scenarios (Table 5, Appendix 2a), which indicates clustered aggregations of canopy trees are more sensitive to have less dispersal events, even with higher tree abundance. Similarly, random fruiting tree distributions with very low tree densities, suffered greatly with the loss of dispersal events (Table 5).

In the case of seed size-GRT scenarios, even though longer distances of dispersal are obtained in the first scenario with smaller seed (therefore smaller GRT; Table 4, fig 11), number of dispersal events do not seem to vary greatly between seed size scenarios (Table 5, Appendix 2b).
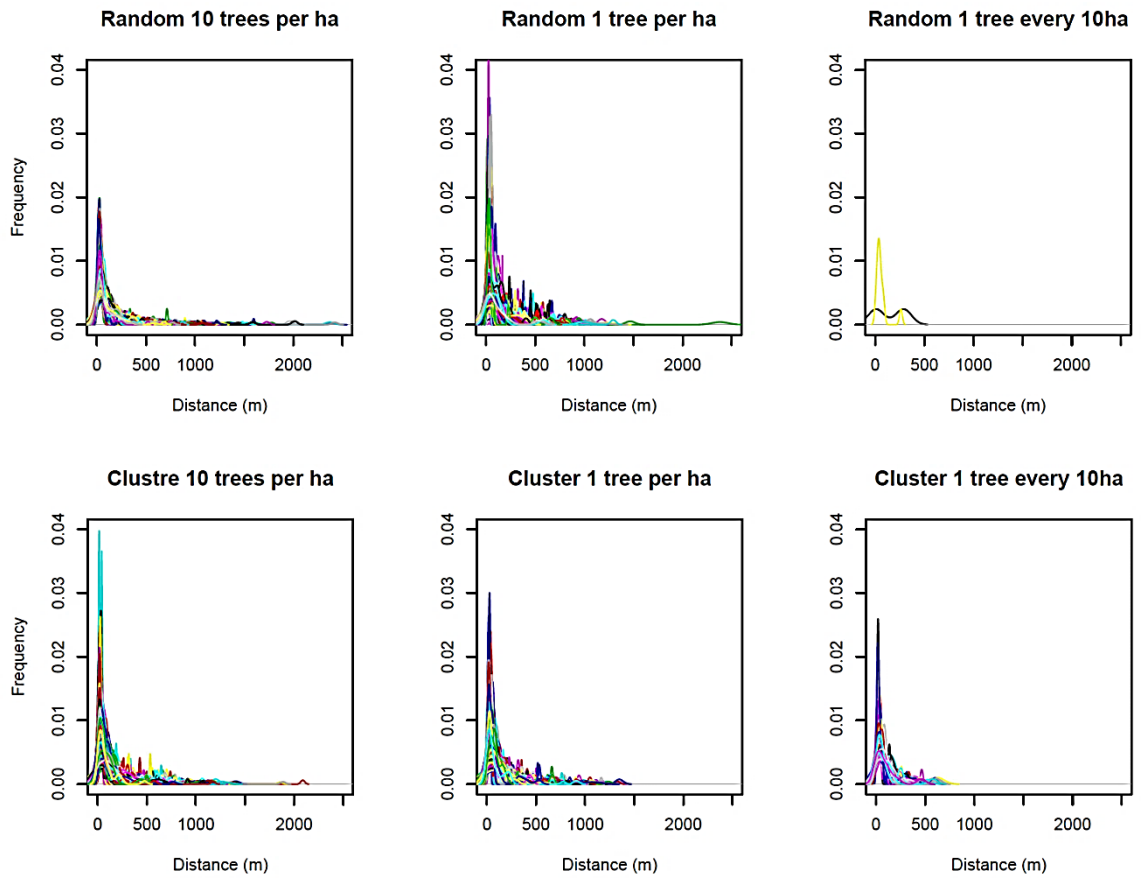
Fig. 10. Seed dispersal distance frequency distributions for six tree abundance and distribution scenarios. All different colored curves represent individual ten thousand simulations that contain more than ten values of seed dispersal events per iteration.
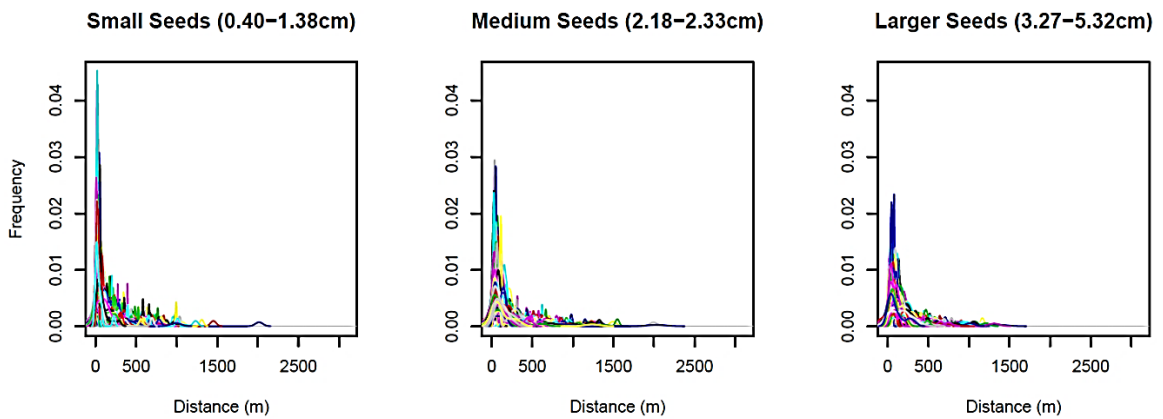
Fig. 11. Seed dispersal distance frequency distributions for three seed size-GRT scenarios. All different colored curves represent individual ten thousand simulations that contain more than ten values of seed dispersal events per iteration.

Table 5. Number of seed dispersal events for every simulated scenario of seed dispersal by howler monkeys.

Scenario	Iterations	Mean	SD	CV	Min	Max	Asymmetry
Random ten trees per ha	10000	39.81	2.92	7.33	16	50	13.63
Random one tree per ha	10000	9.7	3.2	33.01	0	25	3.03
Random one tree every ten ha	10000	1.14	1.27	110.71	0	11	0.90
Cluster ten trees per ha	10000	23.22	17.33	74.62	0	54	1.34
Cluster one tree per ha	10000	7.43	10.96	147.4	0	38	0.68
Cluster one tree every ten ha	10000	1.23	2.38	194.06	0	16	0.52
Small Seed (0.40-1.38cm)	10000	10.06	3.34	33.18	0	24	3.01
Medium Seed (2.18-2.33cm)	10000	8.81	2.75	31.18	0	20	3.20
Large Seed (3.27-5.32cm)	10000	8.24	2.51	30.49	0	20	3.28

Spatial Patterns of Seed Deposition and Latrines

Simulated spatial patterns of seed deposition by howler monkeys (fig. 12) help illustrate seed clustering that exemplify resting or feeding tree sites that become latrines. It also illustrates how some non-latrine depositions are located within these same clusters of seeds; meaning that a monkey could carry seeds from one eating site to another and still disperse them far from the source but not necessarily in dung low density sites. Also, only highly abundant tree scenarios (random and clustered) show significantly aggregated spatial patterns of seed deposition for the simulation evaluated (Appendix 3) for all nine scenarios, mainly because as tree abundance is reduced, so are seed dispersal events and therefore the amount of data is reduced for the K test analysis.
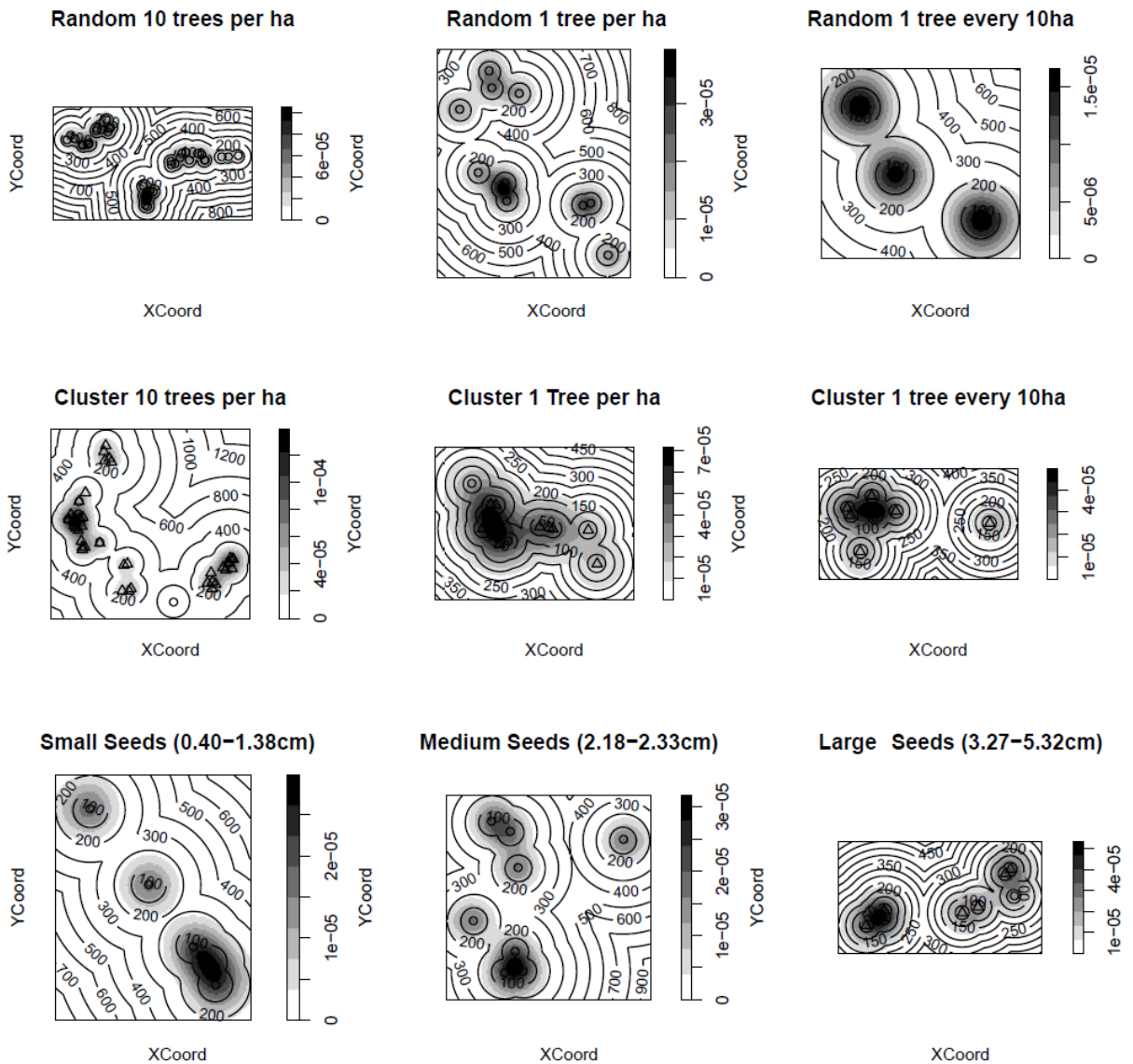
Fig. 12 Howler monkey spatial patterns of seed deposition for one of the ten thousand simulations (that represents the 99th percentile of maximum distances), their associated probability of occurrence, and distances between depositions for six tree abundance and distribution scenarios and three seed size-GRT scenarios. Triangles represent latrine site seed depositions, and circles are non-latrine.

Home ranges obtained from spatial seed deposition patterns (fig. 12) of with minimum convex polygons are shown in Table 6, along with other metrics that could be extracted to help quantify differences between howler monkey seed dispersal scenarios. In this regard it is interesting to see how home range values for all different scenarios tend to follow the same pattern as Euclidean distances (see below).

Table 6. Spatial patterns of seed deposition metrics for one of the ten thousand simulations for nine different scenario (that represents the 99th percentile of maximum distances).

Scenario	Frame Area (ha)	Home Range (ha)	No. Disp. Events	Centroid Mean (m)	No. of Eucl.Dist	Euclidea Mean (m)	SE
Random 10 trees per ha	493.58	157	39	379.50	741	982.05	21.44
Random 1 tree per ha	362.84	94	11	363.27	55	884.05	64.49
Random 1tree every 10 ha	100.06	6	3	275.81	3	580.74	137.93
Cluster 10 trees per ha	558.32	207	45	436.27	990	1077.83	21.99
Cluster 1 tree per ha	91.64	14	13	185.52	78	308.67	20.77
Cluster 1 tree every 10 ha	114.02	21	8	224.41	28	389.68	58.43
Small Seed (0.40-1.38cm)	157.00	3	5	329.21	10	608.91	125.19
Medium Seed (2.18-2.33cm)	230.28	72	8	311.21	28	738.23	70.04
Large Seed (3.27-5.32cm)	118.01	16	9	228.05	36	573.11	61.37

The analysis of Euclidean distances between dispersal events for every spatial patterns of seed depositions (fig. 12) showed that scenarios that have trees with random distribution are significantly different from those with aggregated fruiting tree distributions, except in the case of tree species of clustered aggregations that have very high tree densities per ha (ANOVA: $F_{5,1889}=26.82$, $P<0.0001$; fig. 13A). The third random scenario with lowest abundance of fruiting trees had only three dispersal events; therefore this analysis shouldn't be conclusive for this scenario. On the contrary, the Euclidean distances for scenarios of seed size-GRT do not show statistical differences between them (ANOVA: $F_{2,71}=1.80$, $P=0.1736$; fig. 13B).
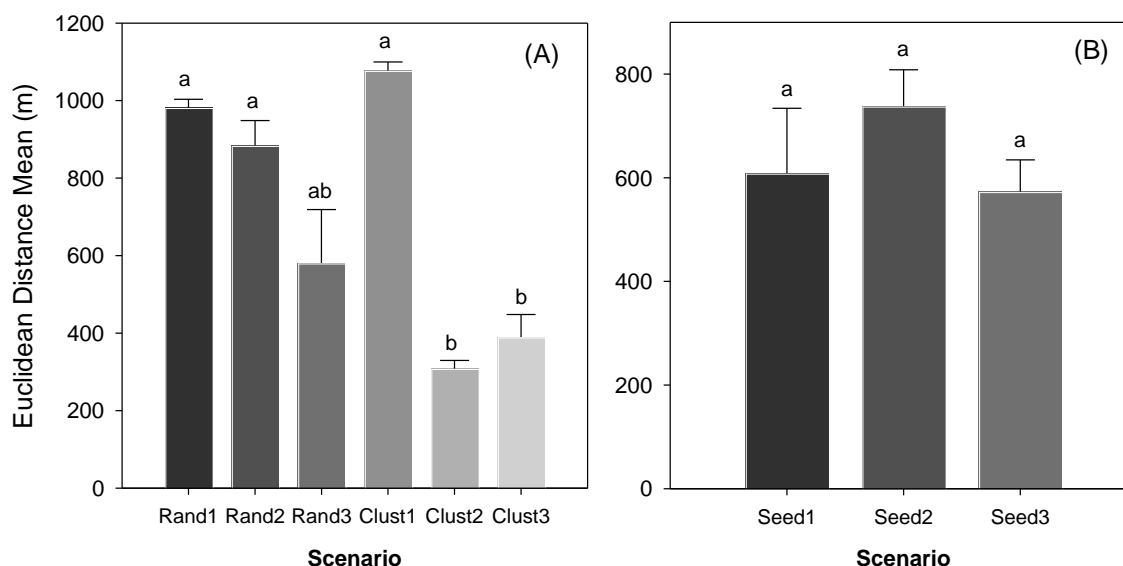
Fig. 13. Mean Euclidean distance reported between every seed dispersal event for each scenarios spatial pattern of seed deposition; bars are standard error. (A) Six different scenarios for reproductive tree abundances and distribution types: scenarios Rand 1, 2, 3, and Clust 1, 2 and 3 symbolize random distribution ten trees per ha, one tree per ha, and one tree every ten ha, and cluster distributions ten trees per ha, one tree per ha, and one tree every ten ha respectively. (B) Three seed size-GRT scenarios: scenarios Seed 1, 2 and 3 signify Small Seed (0.40-1.38cm), Medium Seed (2.18-2.33cm), and Larger Seed (3.27-5.32cm) respectively.

Simple linear regression tests between home range and maximum dispersal distances confirm the existing relationship among these two variables, for all dispersal scenarios except random distribution with the lowest tree density (see Appendix 4), probably due to very few data reported for this scenario (fig. 14 and 15).
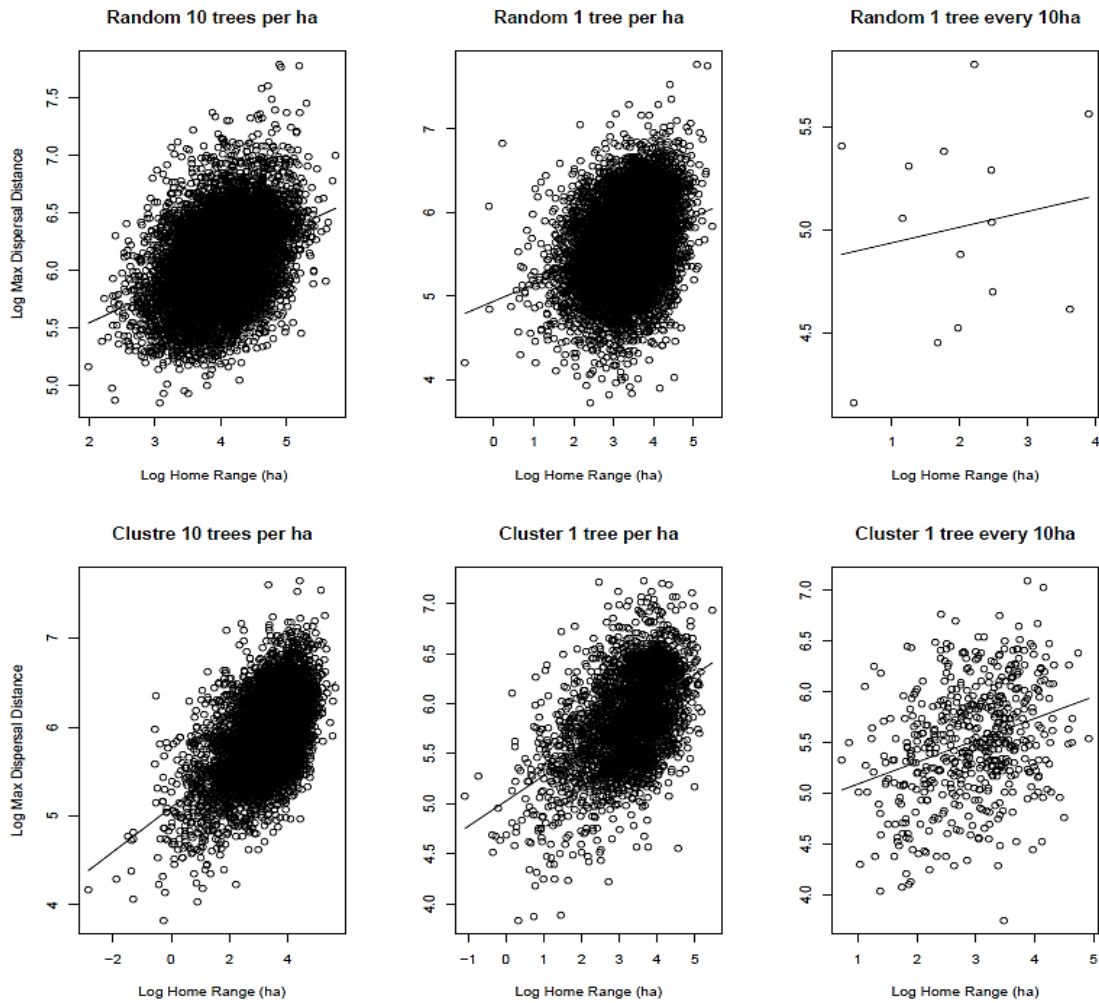
Fig. 14. Linear regressions based on home range and maximum dispersal distances for all simulated tree abundance and distribution scenarios of seed dispersal that contain more than six dispersal events.
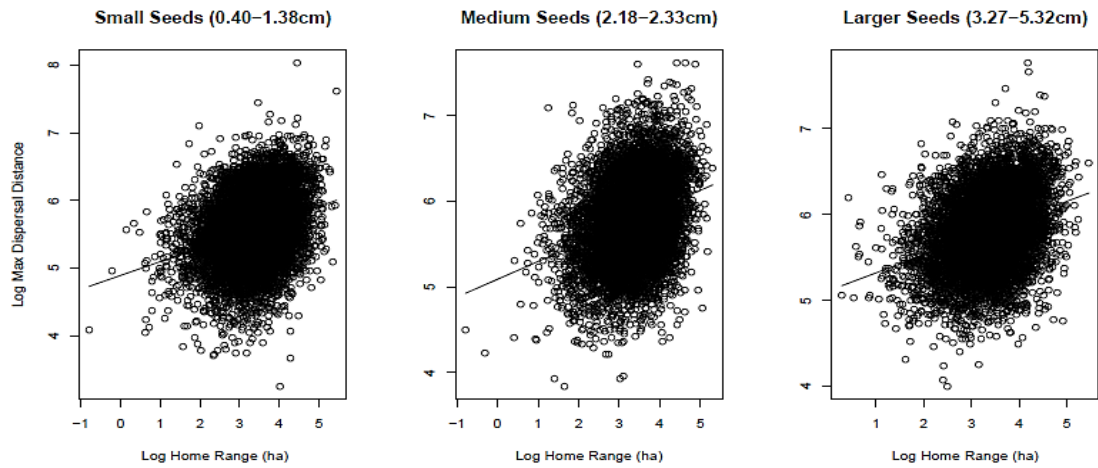
Fig. 15. Linear regressions based on home range and maximum dispersal distances for all simulated seed size-GRT scenarios of seed dispersal that contain more than six dispersal events.

Lastly, highest seed densities from total simulations occurred underneath sleeping sites or latrines (93.6%), and only 6.4% of all seed defecations occurred in non-latrine sites (that could represent the better part of in-transit seed deposition patterns). The long tail of the seed dispersal curves could have resulted from dispersal events under in-transit sites, as seeds dispersed out of latrines (non-latrine) had longer dispersal distances than those in latrines, with a mean distances of seed deposition (maximum distance reported) of 125.74m (2087.8m) and 86.38m (2421.7m) respectively. This difference proved significant within each scenario that was tested (Rand1: t_{27109}=42.1, p<0.001; Rand2: t_{6554}=19.54, p<0.001; Rand3: t_{725}=5.89, p<0.001; Clust1: t_{16314}=34.73, p<0.001; Clust2: t_{5106}=17.73, p<0.001; Clust3: t_{798}=7.32, p<0.001).

It is interesting to see that in the case of seed size-GRT scenarios, even though the total highest seed densities occurred underneath sleeping sites or latrines (86.1%), and 14% of all seed defecations occurred in non-latrine sites; percentages of occurrence varied between scenarios (fig. 16), specially for medium-sized seeds, contrary to tree abundance and distributions scenarios that maintained percentage of occurrence almost identical between scenarios. Regardless, non-latrine seed depositions obtained significantly longest distances compared to latrine sites, with a mean distances of seed deposition (maximum distance reported) of 138.05m (2396.5m) and 110.24m (3094.2m) respectively (Seed1: t_{3057}=12.93, p<0.001, Seed2: t_{43896}=17.88, p<0.001, Seed3: t_{7441}=11.25, p<0.001).
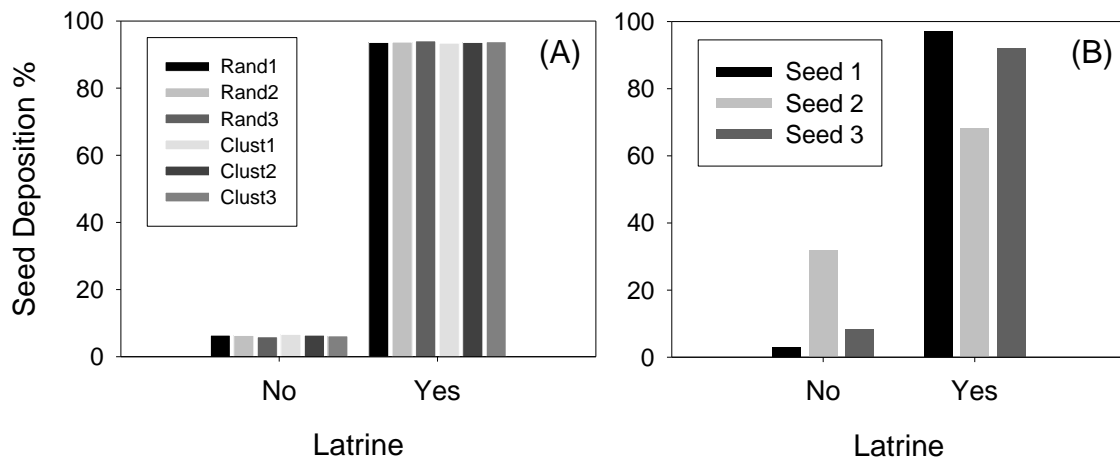
Fig. 16. Percentage of seeds deposited under latrine and non-latrine sites according to all different simulated scenarios of seed dispersal by howler monkeys. (A) Scenarios Rand 1, 2, 3, and Clust 1, 2 and 3 symbolize random distribution ten trees per ha, one tree per ha, and one tree every ten ha, and cluster distributions ten trees per ha, one tree per ha, and one tree every ten ha respectively. (B) Scenarios Seed 1, 2 and 3 signify Small Seed (0.40-1.38cm), Medium Seed (2.18-2.33cm), and Larger Seed (3.27-5.32cm) respectively.

DISCUSSION

Dispersal Distances and Frequency of LDD

Even though seeds that are ingested and dispersed through endozoocory show the longest dispersal distances compared to wind dispersal (Beaudrot et al. 2013), it is clear that most seeds, regardless of the vector, move short distances from the parental canopy (from zero to tens of meters, Howe and Smallwood 1982, Cain et al. 2000, Clark et al. 2005). Consistently to our results, other studies that have implemented mechanistic models of seed dispersal have also obtained leptokurtic, long-tailed kernels (Russo et al. 2006, Viana et al. 2013) that illustrate a strong inclination towards local-scale dispersal.

In the case of our models simulations, local dispersal is interpreted as the values between the 50th percentile and the mean dispersal distances reported for all scenarios, which predict a greater part of seed dispersal events occurring between 60 m and 100 m approximately, while maximum dispersal distances range from 1372-3094 m (Table 4). Previous howler monkey research has indicated mean dispersal distances between 89 and 500 meters (Milton 1980, Estrada y Coates-Estrada 1984, de Figueiredo 1993, Andersen 1999, Julliot 1996, Santamaría-Gómez 1999, Yumoto et al. 1999); and, maximum dispersal distances that have been reported go from 360 to 1200 m (Estrada y Coates-Estrada 1984, Estrada y Coates-Estrada 1991, Julliot 1996, Yumoto et al. 1999, Bravo y Zunino 2000, Bravo 2009). Some of the particular differences with previous studies can be based on the fact that they are empirical data, and most of the extremely low values where collected in fragmented forest.

According to Soons and Ozinga (2005), LDD plays a much more important role in influencing regional survival in plant species than local-distance dispersal. Although there is a

general understanding that LDD is a rare and sporadic event (Nathan 2006), its definition still remains arbitrary and strongly governed by the context of the study (Cain et al. 2000, Levey et al. 2008). Nevertheless, since our goal in this investigation is to have a better understanding of LDD in terms of migration and range expansion for canopy tree species that depend on howler monkeys for dispersal under future climate change scenarios, the 99th percentile of seed dispersal distances simulated give us an objective threshold that can be used for understanding howler monkeys LDD capacity. .

Though differences in LDD distances weren't really clear between random and cluster scenarios of tree abundance and distribution for this investigation, a strong tendency towards the reduction of LDD events is noted for scenarios with low abundance of reproductive trees (Table 4, fig. 10). This statement is also true for total number of dispersal events per simulation (Table 5). Simultaneously, in the case of seed size-GRT scenarios, small seeds presented a greater amount of LDD cases than medium and large sized-seeds (Table 4), but the overall numbers of seed dispersal events were not affected by variation in seed sizes. This suggests that the most important variable impacting seed dispersal events and the occurrence of long-distance seed dispersal events in the case of howler monkeys is the abundance and accessibility of fruit (and therefore seeds), which in this study is evaluated with reproductive tree abundance.

It does not seem odd that reproductive tree abundance (or fruit availability) resulted as the most susceptible variable for seed dispersal and LDD events, since the proximity of one tree to other fruiting trees is one of the extrinsic factors that influences frugivore movement and foraging behavior (Clark et al. 2005, Nathan 2008, Cousens et al 2010, Correa-Cortes and Uriarte 2012). In this regard, one would expect that monkeys with less availability of fruit would have to travel farther and thus promote LDD events; none the less, the greater the accessibility for fruit, the larger the amount of seeds that have a chance to be dispersed and to obtain longer distances of dispersal (Shupp et al. 2010). This result is important in relation to the ecological implications for rare canopy tree species, because their ability for LDD will influence their possibility for regional survival (Soons and Ozinga 2005).

Spatial Patterns of Seed Deposition and Latrines

Aggregation is a dominant and widespread pattern of tree species distribution in tropical and subtropical forest, which can be shaped by dispersal limitations among other mechanisms (Lin et al. 2009). Furthermore, animal-dispersed plant species show more clumped seed depositions in comparison to other dispersal syndromes (Muller-Landau et al. 2008), but howler monkeys contribute to the production of the largest aggregations of dung (and therefore seeds if fruit is consumed) among Neotropical arboreal mammals (Julliot 1996, Yumoto et al. 1999, Bravo & Zunino 2000, Andresen 2002, Bravo 2009). Consistently, our simulated spatial patterns of seed depositions coincide with the aggregation referred to by other authors, except in the case of low density fruiting trees, where fecal matter does not seem to be aggregated due to lower deposition densities (Table 6, Appendix 3).

The illustration of spatial patterns of seed deposition allows better comprehension of density and probability of seeds being deposited under certain sites, but also of "microsite" depositions (Correa-Cortes and Uriarte 2012) or secondary latrines in the case of howler monkeys. In our case, these microsites can be explained by the small degree of multimodality observed in individual simulations frequency distributions (fig. 10 and 11), that may represent aggregation beneath sleeping sites at different distances from parental trees

(Russo et al. 2006). Basically, greater seed clustering for howler monkeys embodies sleeping tree sites that become latrines (Julliot 1996, Bravo & Zunino 2000, Bravo 2009); at the same time, low seed densities can happen by defecation of single individuals (Andersen 2002, Bravo 2012) during "in-transit" movements, that may also explain LDD events (Russo et al. 2006). In this sense, our model successfully accounts for clumped patterns of seed deposition by howler monkeys with the addition of its scattered component, as demonstrated by Bravo (2009).

Interestingly enough, our seed dispersal plots illustrate how some non-latrine depositions are located within the same clusters of seeds that represent latrines; meaning, a monkey could carry seeds from one eating or resting site to another and still disperse them far from the source but not necessarily in low-density dung sites. In this regard, Bravo (2009) also mentions how howler monkeys can roam across their home ranges during the day, to eventually return to their starting point or main sleeping tree; explaining non-latrine depositions within latrine areas.

As our analysis of variance of Euclidean distances of spatial seed deposition patterns shows, distribution of food resources or the arrangement of fruiting trees in space (in the case of this study) has an effect on spatial patterns of seed deposition; except in the case of very high density of fruiting trees (10 trees per ha in clustered scenario), in which case spatial patterns don't show differences between tree distribution (fig. 13A). In this respect, Correa-Cortes and Uriarte (2012) emphasized that seed deposition patterns arise from the interaction of animal behavior and food distribution in time and space. Cousens et al. (2010), also highlights that the way animals move and deposit seeds are the result of the influence that arises from the relationship that intrinsic (social behavior, GRT) and extrinsic factors (fruit distribution, abundance, landscape structure) play, and has to be taken into account when simulating seed dispersal patterns. This said, seed size (hence GRT) appears to have no real effect on the distribution of seed deposition in space, at least within the reach of this study.

Correa-Cortes and Uriarte (2012) states that an animal's movement is largely limited by its home range area. Bravo (2009), also confirmed in her study in Argentina that differences in seed dispersal distances reflected dissimilarities in the spatial use of the forest by howler monkeys. Consistently, our calculated approximations of home range values show a significant effect over maximum distances of seed dispersal for overall simulations in all scenarios in this investigation; however, home range area cannot be presumed to explain LDD on its own, as many other factors come into play. Low fruiting tree abundance, for instance, seems to affect this relationship more than seed size.

The proportion of latrine depositions was tremendously high for howler monkey simulations for all scenarios (94% and 86% respectively), in contrast with previous howler monkey studies, where percentage of latrine defecations range between 61% and 75% of deposition events (Julliot 1996, Andersen 2002, Bravo 2009). Differences with literature may be due to the fact that our study is based on a model that is affected by the behavior of its parameters; GRT, as explained below, impacts the proportion of latrine depositions; as does a subset of parameters that are constant during all simulations, like the time of day when we decide a monkey starts its daily activities (*Tday*), which in our case, by default is at 6 am. Nevertheless, it is clear that latrines comprise most defecation events, and some studies have revealed that latrines appear to be important sites for recruitment of the most common tree species, and some rare species as well (Anzures-Dadda et al. 2011, Bravo 2012).

The only variable that seed size affected in our study, is the proportion of seeds defecated over latrine and non-latrine sites. It is clear that distances of dispersal are significantly longer in non-latrine locations because, as stated earlier, "in-transit" seed deposition may also account for LDD events (Russo et al. 2006). As it is, our model indicates that medium-sized seeds have a greater probability of being deposited in non-latrine or in-transit sites because their 22-23 hour range of GRT is accountable for howlers defecating farther from their sleeping trees. Furthermore, the 25-30 hour GRT related to large seeds, as well as the 18-20 hour GRT associated with small seeds appear to coincide with the monkeys sleeping time, augmenting latrine defecation probabilities.

These results are important because tree species with small seeds usually rely on an extensive spectrum of dispersal vectors that benefit and compensate one another; but as seed size increases, the diversity of dispersers decreases (Bueno et al. 2013), converting howler monkeys into one of the few dispersers in charge of large seeded species fate. Two medium-sized seed species that can be dispersed by howlers and are found in our study site are *Minquartia guianensis* and *Pouteria reticulata;* both of these are hardwood tree species. Further studies must be made to understand the consequences for medium and large seeded canopy tree species.

The Howler Monkeys Role in Seed Dispersal and Implications for Conservation

Even though some studies have shown that howlers are able to disperse large amounts of seeds (Estrada and Coates-Estrada 1984, Julliot 1996) folivory rather than frugivory is their characteristic diet (Reid 2009). In this respect, it is important to consider that highly frugivorous animals are not necessarily better or more effective dispersers than opportunistic frugivores (Wenny 2001), because, in the case of howlers, their generalistic feeding behavior qualifies them to survive in changing environments with variation in food resources (Beasudrot et al. 2013). And even if the majority of their seed defecations end up in high-densities supporting local dispersal, its ecological importance should not be under-estimated, as the more effective the dispersal at a local level, the greater the likelihood that dispersion between metapopulations is effective (Schupp et al. 2010).

Some studies have already categorized primates to belong to their own functional group apart from birds (Clark 2001, Beasudrot et al. 2013), but also have recognized that the community structure of tree associations that depend on primate dispersal are bound by dispersal limitations; because even though highly mobile, most monkeys will spend the greater part of their existence in the same area (Beasudrot et al. 2013). Schupp et al. (2010) recognize that although there are dispersal agents and dispersal assemblies of species (or functional groups of seed dispersers) that are more efficient than others, it is important to take into account that the *merged seed dispersal patterns* of all, determine the resilience of the dispersal system, and the possibility of LDD events. That is why, even if *Alouatta* species aren't able to produce LDD of 100km (or longer) like migratory birds (Viana et al. 2013), their contribution and overall effect on forest structure should be noted.

Forest landscape fragmentation and climate change threaten the survival of our natural habitats (Pakeman 2001, Bertin 2008, Engler and Guisan 2009). Even though howler monkeys are considered persistent in disturbed habitats, Arroyo-Rodriguez and Dias (2009) have found evidence that high proportions of territory fragmentation and degradation do in fact adversely affect this species survival, mostly due to the reduction in food accessibility. Also, the bigger the forest area, the farther the monkeys will be able to move, increasing the

probability for LDD, successful germination and establishment; whereas in small fragments seeds have a higher probability of being deposited under adverse conditions (Serio-Silva and Rico-Gray 2002).

In time, the pressures of habitat reduction and hunting will affect howler monkey numbers, which will in turn have major ramifications on seed dispersal and the alteration of seedling communities, and thus recruitment of large-seeded tree species (Muller-Landau 2007, Beasudrot et al. 2013). We are looking at a scenario were these human-altering consequences distress the adaptation of those natural processes at the very time that climate change requires a responsive velocity for plant species to migrate to more suitable environments (Clark et al. 1998, Higgins and Richardson 1999, Beasudrot et al. 2013); especially those large-seeded low density canopy tree species that have aggregated distributions.

Future development of the MonkeySeed Model

Our simulation model of seed dispersal by howler monkeys (*Alouatta sp.*) has a few key areas for future development. In first place it is important to remember that seed deposition patterns pertain to just one simulated monkey, even though howlers live in cohesive social groups (a mean of 4-16 individuals per group has been reported, Chivers 1969, Mittermeier 1973, Gaulin et al. 1980, Braza et al. 1981, Estrada 1982, Garcia 1993, Amato y Estrada 2010, Pavelka y Knopff 2004); concurrently, we do not take into consideration the amount of seed being ingested nor excreted, only the frequency of seed being consumed, and therefore expelled. Secondly, although we base our monkeys movement simulations on real field angle and velocity input data, radio-taking records would be most efficient for realistic seed dispersal simulations, as would be to include the position and number of attractive sites in howler monkeys habitats, as a means to embrace an animal's intentional trajectory movements through space (Will and Tackenberg 2008, Cousens *et al.* 2010, Correa-Cortes y Uriarte 2012). Finally, the inclusion in the model of landscape structure like dispersal barriers and altitudinal gradients should be considered for further studies.

Conclusions from Our Model

Our models results are highly influences by the behavior of its parameters. In terms of the parameters obtained by literature review, variation in the values and probability of occurrence of these values can be due to differences in the origin of the data (studies of very diverse contexts), or to the need of obtaining more information on the time that howler monkeys invest in their daily activities and their digestion. Interesting enough, the distribution of the values of movement angles that we obtained in the field do not reflect the patterns of travel movement or trails that these animals have; suggesting that more data must be obtained to make better conclusions. And, even if a sensitivity analysis was not conducted for our parameters, GRT proved to be the most sensitive parameter for longest dispersal distances as seen with medium-sized seeds; as well as fruiting tree abundance resulted most sensitive to the number of seed dispersal events.

Our motivation for the development of this model is to generate information that can help guide actions for the adaptation of climate change. This is why the results of dispersal distances generated with our *MonkeySeed* model can be applied in other modeling tools that

incorporate local and long distance dispersal distances to simulate canopy tree species distribution and migration across time, space, and future climate change scenarios.

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10. COMPLEMENTARY CHAPTER:

Concentration in Development Practices

10.1 Analysis of the Results of this Study and their Implications for Human Development

Ecosystem services are functions provided by nature that improve and sustain human wellbeing. In this regard, seed dispersal represents a key life support function in ecosystems that allows nature to regenerate and adapt to changes in landscapes and climatic conditions, permitting canopy tree species (among many other plant species) to establish, disperse, and migrate throughout natural and disturbed landscapes if possible. Seed dispersal is an ecosystem service that is produced at a local scale (in most cases) by mobile organisms (dispersal agents) foraging within or between habitats; and, although these mobile organisms deliver services locally, their individual behavior, population biology and community dynamics are often affected by the spatial distribution of resources at a larger landscape scale.

In this regard, howling monkeys represent an effective seed dispersal agent, since they are one of the largest Neotropical primates (allowing them to eat more and to swallow bigger seeds), and they generally show the highest density among primate populations; also, the proportion of fruit in the howler diet goes from 10 to 60% which makes them an important seed disperser. More importantly, howler monkeys are often the only large seed dispersal agents that may survive for a long time in small forest fragments and thus may play a crucial role in plant regeneration processes.

So the question remains: what are the implications, effects or consequences of the results obtained in this study for the different dimensions of human development?

For the natural or environmental dimension of development, the implications of this study are inarguable; seed dispersal by howler monkeys contributes tremendously to the structure and composition of forests and their regeneration. Specifically, this study supports howling monkeys in their influence on seed deposition patterns and seed dispersal distances that may be critical for some species of canopy trees that do not have a great range of dispersal agents, that have medium to large sized seeds, and that have low density aggregation patterns of establishment throughout the forest. And even if the majority of their seed defecations end up in high-densities supporting local dispersal, its ecological importance should not be under-estimated, as the more effective the dispersal at a native level, the greater the likelihood that dispersion between metapopulations is effective.

Since howler monkeys disperse a great part of the most abundant tree species of Neotropical forests, it is safe to say that their contribution to structure and tree species configuration of forests sets the pattern for many ecosystem services that originate from the ecological interactions of dominant species in forest cover. Ecosystem services that can be affected by forest structure and species composition are related to aquifer recharge, soil quality and composition, carbon dioxide sequestration, and production of natural resources, among others.

Therefore, at a local and regional scale, if howler monkeys cease to exist, or if their contribution to seed dispersal is cut short due to deforestation and fragmentation of their natural habitats, the distribution and abundance of many natural resources derived from canopy tree species that are dispersed by these mobile organisms will suffer the consequences. Many of the tree species that are dispersed by howling monkeys represent community capitals, because of their wood, fruits, or other parts of the trees used for medicinal purposes; this is why at a cultural and social-economical level or dimension, communities that have had traditional use of these tree species could be affected. Therefore, interactions between the primate species and the plant community are highly relevant to conservation purposes.

Also, howling monkeys have become an emblematic species for tropical forest conservation and tourism, and local people are used to coexisting with these animals wherever they inhabit. Meaning, that the mere presence of these primates represents a cultural, social and economic capital for many communities that live amongst the natural conditions that support their coexistence.

If people understood the important role that fruit-eating animals play in the regeneration of the forest and consequently the natural adaptation of changing habitats and the distribution and abundance of many natural resources and important ecosystem services, it would seem that bigger efforts for conservation and landscape connectivity would take place. In rural communities, for example, where people are most dependent on natural capitals, environmental awareness of the importance of big-sized mammals as seed dispersers and their contribution to the natural expansion of their environments should be applied constantly, especially as hunting and deforestation are usual activities that harm sustainable development, and can threaten the coexistence of human communities in natural environments and their ability to extract resources with all their right.

10.2 Analysis of the Results of this Study for the Potential of New Policy Creation.

Forest landscape fragmentation and climate change threaten the survival of our natural habitats. And, even though howler monkeys are considered persistent in disturbed areas, there is recent evidence that a high proportion of territory fragmentation and degradation does in fact adversely affect this species survival, mostly due to the reduction in food availability. As it is, the bigger the forest area, the farther away the monkeys will be able to travel, increasing the probability for long-distance dispersal, successful germination and establishment of trees; whereas in small forest fragments seeds have a higher probability of being deposited under unbefitting conditions.

Additionally, in recent years it has become evident that the presence of streets, roads and power lines, not only fragment natural habitats and decrease range distribution for many wild life species, but also represent a deadly obstacle for many large-sized, fruit-eating terrestrial and arboreal seed dispersers like monkeys, tapirs, coatis, bats, kinkajous, raccoons, opossums, tayras, porcupines, coyotes, iguanas, and many species of birds.

Without mentioning other endangered wild life creatures like ocelots, jaguarundis, and peccaries that meet their doom more frequently than can be expected.

Every year hundreds of wild animals die killed on the roads, accelerating the process of extinction for some species that are already threatened. These deaths occur primarily by the development of roads and streets that go across biological corridors and National Parks, because of inadequate planning in the creation of these pathways.

In time, the pressures of habitat reduction, hunting, and road-kill will affect howler monkey numbers (amongst other important wild life species), which will in turn have major ramifications on seed dispersal and the alteration of seedling communities, and thus recruitment of large-seeded trees. We are looking at a scenario were these human-altering consequences distress the adaptation of those natural processes at the very time that climate change requires a responsive velocity for plant species to migrate to more suitable environments; especially those large-seeded low density canopy species that have aggregated distributions.

So, what can be done? In what way might this study's findings be used to influence decision making and policy formation for this existing problem?

This study has revealed once more the importance of howler monkeys as effective seed dispersers, especially for more susceptible canopy large-seeded tree species of reduced abundance. And even if we haven't addressed the importance of other large-sized arboreal mammals as seed dispersers, their vulnerability to fragmentation, hunting, and anthropogenic infrastructure is still eminent.

At a local level, communities and municipalities can join efforts to prevent loss of connectivity for arboreal seed dispersers buy creating comities and obtaining funding for projects that promote investigation of the harm that is being caused, and the creation of solutions for these problems. Some local organizations have already started to take action in these matters; *Coopeguanacaste* with the University of Costa Rica and *SalveMonos* have worked towards better understanding where and how howlers are dying, restoring natural habitats and constructing wildlife aerial crossings for monkeys and other arboreal species in the Guanacaste region.

At a national level, some policies could also be made. More and better planning should take place in the design and construction of roads and highways, especially in hi-mortality zones that border and cut through protected areas. Biological studies that map and take into account animal populations should be required previous to the approval of roadways and electrical projects; that way the decision of where to implement mitigation solutions would have better criteria, and wildlife genetics and ecosystem health aspects can be included in human development projects.

Additional prevention efforts may be made to the existing electrical infrastructure, signalization on the roads, and the implementation of wildlife crossings should be mandatory in hi-pressure zones. In the case of howler monkeys, for example, the application of aerial bridges represents a great way to prevent deaths, allowing permeability at a local and landscape level.

11. APPENDIX

Appendix 1. Howler monkey literature review for model parameters.

PARAMETER		VALUE	SPECIES	CONT.	FRAG.	COUNTRIE	REFERENCES
Feeding Time Invested in Day	Young Leaves	46.70%	*A. palliata*		X	Mexico	Estrada et al. 1999
		32.8 - 49.6%	*A. palliata*		X	Mexico	Dunn et al. 2009
		21.30%	*A. palliata*	X		Costa Rica	Chapman 1988
		62 - 65%	*A. palliata*	X		Costa Rica	Stoner 1996
	Mature Leaves	8.7-15.5%	*A. palliata*		X	Mexico	Dunn et al. 2009
		27.70%	*A. palliata*	X		Costa Rica	Chapman 1988
		2 - 6%	*A. palliata*	X		Costa Rica	Stoner 1996
	Leaves General	74.00%	*A. fusca*		X	Brazil	Garcia 1993
		49.00%	*A. palliata*	X		Costa Rica	Chapman 1988
		58.62%	*A. pigra*		X	Belize	Pavelka y Knopff 2004
		43.40%	*A. belzebul*	X		Brazil	Pinto et al. 2003
	Fruit	34.80%	*A. palliata*		X	Mexico	Estrada et al. 1999
		39.1 - 49.4%	*A. palliata*		X	Mexico	Dunn et al. 2009
		50%	*A. palliata*	X		Mexico	Estrada y Coates-Estrada 1984
		6.90%	*A. fusca*		X	Brazil	Garcia 1993
		17.60%	*A. caraya*	X		Argentina	Bravo y Sallenave 2003
		28.50%	*A. palliata*	X		Costa Rica	Chapman 1988
		17 -29%	*A. palliata*	X		Costa Rica	Stoner 1996
		41.38%	*A. pigra*		X	Belize	Pavelka y Knopff 2004
		44.00%	*A. seniculus*	X		Peru	Andersen 1999
		43.90%	*A. belzebul*	X		Brazil	Pinto et al. 2003
	Flowers	2.50%	*A. palliata*		X	Mexico	Estrada et al. 1999
		1.0 -2.2%	*A. palliata*		X	Mexico	Dunn et al. 2009
		12%	*A. caraya*	X		Argentina	Bravo y Sallenave 2003
		23%	*A. palliata*	X		Costa Rica	Chapman 1988
		6 -11%	*A. palliata*	X		Costa Rica	Stoner 1996
		13%	*A. belzebul*	X		Brazil	Pinto et al. 2003
	Total Feeding Time	17%	*A. palliata*		X	Mexico	Estrada et al. 1999
		27.7 - 17.7%	*A. palliata*		X	Mexico	Dunn et al. 2009
		13.30%	*A. palliata*		X	Panama	Bernstein 1964
		16.90%	*A. palliata*		X	Nicaragua	Garber y Jelinek 2006
		18.00%	*A. fusca*		X	Brazil	Garcia 1993
		16.80%	*A. palliata*		X	Panama	Mittermeier 1973
		18.90%	*A. caraya*	X		Argentina	Bravo y Sallenave 2003
		18.57%	*A. pigra*		X	Belize	Pavelka y Knopff 2004
		18.00%	*A. seniculus*	X		Peru	Andersen 1999
		23.32%	*A. seniculus*	X		Colombia	Yumoto et al. 1999
		21.80%	*A. seniculus*	X		Venezuela	Braza et al. 1981

Category	Value	Species			Country	Reference
Rest Time Invested in Day	80%	*A. palliata*		X	Mexico	Estrada et al. 1999
	53.7 - 68.2%	*A. palliata*		X	Mexico	Dunn et al. 2009
	16.40%	*A. palliata*		X	Panama	Bernstein 1964
	73.00%	*A. palliata*		X	Nicaragua	Garber y Jelinek 2006
	64%	*A. fusca*		X	Brazil	Garcia 1993
	73%	*A. palliata*		X	Panama	Mittermeier 1973
	57%	*A. caraya*	X		Argentina	Bravo y Sallenave 2003
	66%	*A. pigra*		X	Belize	Pavelka y Knopff 2004
	49%	*A. belzebul*	X		Brazil	Pinto et al. 2003
	63%	*A. seniculus*	X		Peru	Andersen 1999
	62%	*A. seniculus*	X		Venezuela	Braza et al. 1981
Movement Time Invested in Day	3%	*A. palliata*		X	Mexico	Estrada et al. 1999
	14.9 - 10.2%	*A. palliata*		X	Mexico	Dunn et al. 2009
	25.30%	*A. palliata*		X	Panama	Bernstein 1964
	9.10%	*A. palliata*		X	Nicaragua	Garber y Jelinek 2006
	13.00%	*A. fusca*		X	Brazil	Garcia 1993
	10.50%	*A. palliata*		X	Panama	Mittermeier 1973
	10.50%	*A. caraya*	X		Argentina	Bravo y Sallenave 2003
	7.49%	*A. pigra*		X	Belize	Pavelka y Knopff 2004
	9.00%	*A. seniculus*	X		Peru	Andersen 1999
	16.60%	*A. seniculus*	X		Venezuela	Braza et al. 1981
Digestion Time Invested in Day	18 h	*A. palliata*	X		Mexico	Estrada y Coates-Estrada 1984
	16-25 h	*A. palliata*	X		Costa Rica	Wehncke et al. 2004
	18-20 h	*A. palliata*	X		Mexico	Estrada y Coates-Estrada 1991
	20-30 h	*A. palliata*	X		Mexico	Serio-Silva y Rico-Gray 2002
	20.4 h	*A. palliata*			Costa Rica	Pruetz et al. 1996
	19 h	*A. guariba*		X	Brazil	Martins 2006
	35 h	*A. seniculus*	X		Guiana	Julliot 1996
	35 h	*A. seniculus*	X		Colombia	Stevenson et al. 2002
	19.66 h	*A. seniculus*	X		Colombia	Yumoto et al. 1999
% Feces in Latrine	65%	*A. caraya*	X		Argentina	Bravo 2009
	75%	*A. seniculus*	X		Brazil	Andersen 2002
	61%	*A. seniculus*	X		Guiana	Julliot 1996
% Scatered Feces (in in-transit sites)	35%	*A. caraya*	X		Argentina	Bravo 2009
	18.50%	*A. seniculus*	X		Guiana	Julliot 1996
	26%	*A. seniculus*	X		Brazil	Andersen 2002
Home Range	5.8 - 89.5 ha	*A. palliata*		X	Mexico	Dunn et al. 2009
	60 ha	*A. palliata*	X		Mexico	Estrada y Coates-Estrada 1984
	33 ha	*A. palliata*	X		Mexico	Amato y Estrada 2010
	45 ha	*A. seniculus*	X		Guiana	Julliot 1996
	1.7 - 2.2 ha	*A. caraya*	X		Argentina	Bravo y Sallenave 2003
	35 -54 ha	*A. palliata*	X		Costa Rica	Stoner 1996
	60 ha	*A. palliata*	X		Mexico	Estrada 1984

	75 ha	*A. palliata*	X		Mexico	Serio-Silva y Rico-Gray 2002
	108 ha	*A. palliata*	X		Costa Rica	Chapman 1988
	17.8 ha	*A. belzebul*	X		Brazil	Pinto et al. 2003
	15.3 ha	*A. pigra*	X		Belize	Gavazzi et al. 2008
Day Movement Ranges	395.3- 241.6 m	*A. palliata*		X	Mexico	Dunn et al. 2009
	451.5 m	*A. palliata*	X		Mexico	Estrada y Coates-Estrada 1984
	202 m	*A. palliata*	X		Mexico	Amato y Estrada 2010
	100-200 m	*A. palliata*		X	Panama	Bernstein 1964
	100-150 m	*A. palliata*		X	Panama	Mittermeier 1973
	381 m	*A. palliata*		X	Nicaragua	Garber y Jelinek 2006
	513 -602 m	*A. caraya*	X		Argentina	Bravo y Sallenave 2003
	683.5 m	*A. belzebul*	X		Brazil	Pinto et al. 2003
	284.39 m	*A. palliata*		X	Panama	Chivers 1969
	700 m	*A. seniculus*	X		Guiana	Julliot 1996
	980 m	*A. seniculus*	X		Colombia	Yumoto et al. 1999
Mean Individuals per Family Group	16.20	*A. palliata*		X	Panama	Mittermeier 1973
	6.3	*A. seniculus*	X		Venezuela	Braza et al. 1981
	6.6	*A. pigra*		X	Belize	Pavelka y Knopff 2004
	4.9	*A. fusca*	X		Brazil	Garcia 1993
	14.7	*A. palliata*		X	Panama	Chivers 1969
	5 -16	*A. palliata*	X		Mexico	Amato y Estrada 2010
	8.33	*A. palliata*		X	Panamá	Gaulin et al. 1980
	9.12	*A. palliata*	X		Mexico	Estrada 1982
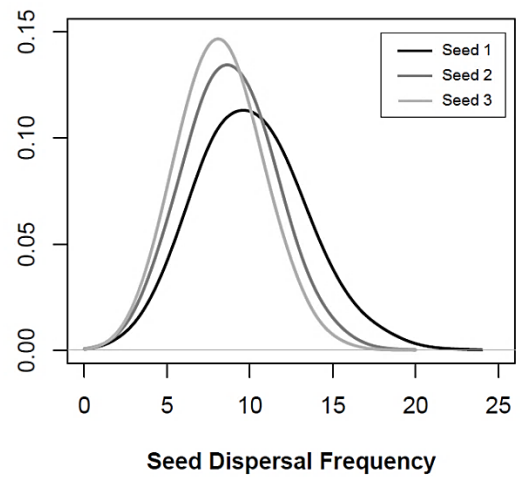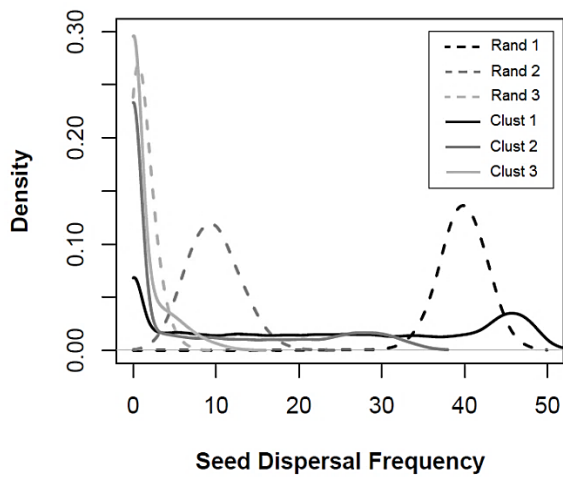
Appendix 2. Number of dispersal events for every simulated scenario. Graphic (a) represents 6 different scenarios for reproductive tree abundances and distribution types: scenarios Rand 1, 2, 3 symbolize random distributions with ten trees per ha, one tree per ha, and one tree every ten ha; and Clust 1, 2 and 3 symbolize clustered distributions with ten trees per ha, one tree per ha, and one tree every ten ha respectively. Graphic (b) represents three GRT scenarios depending on three different seed ranges of sizes: scenarios Seed 1, 2 and 3 signify Small Seed (0.40-1.38cm), Medium Seed (2.18-2.33cm), and Large Seed (3.27-5.32cm) respectively.
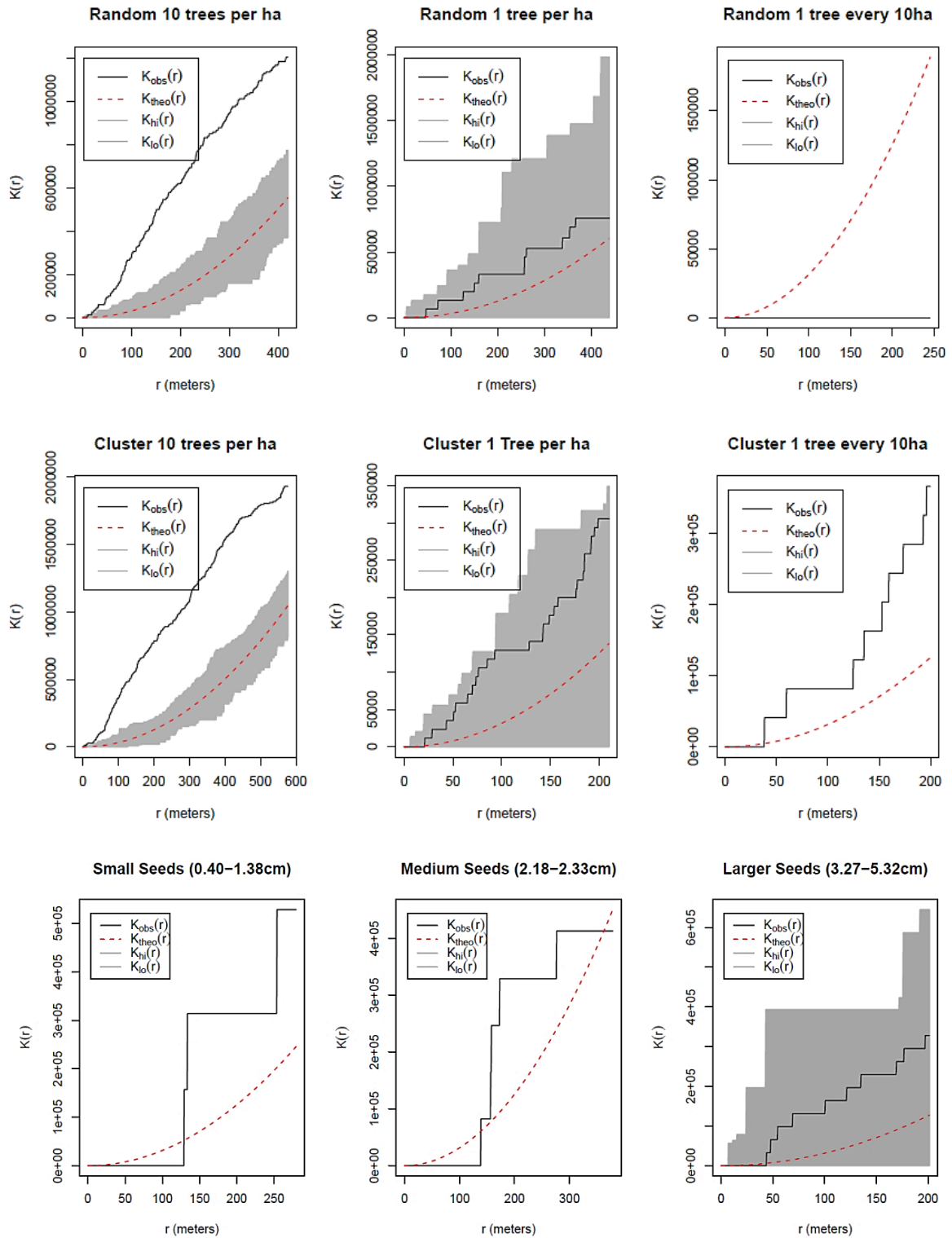
Appendix 3. K estimation for all nine scenarios of howler monkey seed dispersal simulated. Deviations between the empirical and theoretical *K* curves may suggest spatial clustering or spatial regularity.

Appendix 4. Estimated home range (minimum convex polygons) areas for total iterations and all scenarios simulated that contain more than 6 dispersal events, used to calculate linear regressions between home range and maximum dispersal distance log values. The table shows mean values for home range and maximum dispersal distances, minimum and maximum dispersal distances, and linear regression test values.

Senario	Home Range Mean (ha)	Max Distance Mean	Min	Max	p-value	R^2	F	df
Random 10 trees per ha	63.48	468.00	126.9	2421.7	0.0001	0.14420	1686.0	9998
Random 1 tree per ha	36.264	311.69	41.04	2380.62	0.0001	0.08257	758.6	8417
Random 1tree every 10 ha	11.858	166.07	63.76	331.51	0.5726	-0.05379	0.3	12
Cluster 10 trees per ha	41.59252	416.45	45.79	2087.84	0.0001	0.29840	3145.0	7392
Cluster 1 tree per ha	37.1054	387.02	46.22	1371.67	0.0001	0.24560	1089.0	3339
Cluster 1 tree every 10 ha	25.017	284.41	42.26	1198	0.0001	0.09322	57.0	544
Small Seed (0.40-1.38cm)	36.8718	299.9	25.71	3094.18	0.0001	0.08290	779.2	8608
Medium Seed (2.18-2.33cm)	35.4519	366.7	46.39	2031.09	0.0001	0.08514	745.0	7994
Larger Seed (3.27-5.32cm)	35.699	369.1	54.50	2361.8	0.0001	0.09999	833.1	7488

Appendix 5. *MonkeySeed* MODEL *Script* for R (R Development Core Team 2011)

```
#SET PARAMETERS (Directory, name and values will depend on every user)

getwd()
setwd("C:/modelo")

escenarios<-read.table('escenarios.txt', sep=',', header=T)
HR<-read.table('HR_uniformes.txt', sep=',', header=T)
Para<-read.table('Parametros1.txt', sep=',', header=T)
Vel.Ang<-read.table('Vel.Ang.txt', sep=',', header=T)

#PARÁMETROS
XYini<-HR
Vtray<-Vel.Ang[,1]
Atray<-Vel.Ang[,2]
Tmov<-Para[,1]
Tfeed<-Para[,2]
Trest<-Para[,3]
Tdig<-Para[,4]
XYseed<-escenarios[,c(1,2,3)]
It<-10000
Tsimul<-2*30*24*60
radio<-20
Tday<-780
Tnight<-660
directory<-"C:/modelo/"
file<-"ESC1.RData"
```

```
# MODEL

Traj_monkeys<-function(XYini, Vtray,Atray, Tmov, Tfeed, Trest,Tdig, XYseed,
It,  Tsimul,radio,  Tday,  Tnight,  directory,  file)                #XY,
It,ANG,tiempo,velocidad, ncoord, Semillas
{
setwd(directory)
TablaG<-list()
BW<-as.data.frame(matrix(nrow=It, ncol=2))
colnames(BW)<-c('ID','ECM')
TablaG1<-as.data.frame(matrix(nrow=It, ncol=2))
colnames(TablaG1)<-c('ID','Frequency')
for(j in 1:It) ##número de ciclos
  {
    TablaXY=as.data.frame(matrix(nrow=1000, ncol=5))
    colnames(TablaXY)<-c('ID','CoordX', 'CoordY','Iseed', 'Tdiges')

    TSeed<-as.data.frame(matrix(nrow=1000, ncol=5))
    colnames(TSeed)<-c('CoordX', 'CoordY','DistExc', 'Seed_Exc','Letrinas')

    Xini<-c()
    Yini<-c()
    Vt<-c()

    FILAS<-c(1:length(XYini[,1]))
    cont=sample(FILAS,  1,replace =T)  ##vector  con  probabilidades  para
iniciar las trayectorias o seleccionar las coordenadas de inicio
    Xini<-XYini[cont,1] #Coordenada X de inicio de la trayectoria
    Yini<-XYini[cont,2] #Coordenada Y de inicio de la trayectoria
```

```
    Dis<-c() #Distancia de desplazamiento
    X1<-c() #posición X de la trayectoria
    Y1<-c() #posición Y de la trayectoria
    A<-c()  #Angulo
    Per<-c() #periodo logico
    TDig<-c() ##estimando el tiempo de digestión
    l<-c() # distancia de semilla a la posición del mono
    l1<-c() # número de semillas ingeridas por el mono
    Td<-c() #tiempo del día
    Tc<-c() #tiempo de comer
    Trest1<-c()# tiempo de descanso extraído  por el sample
    Tca<-c() #Tiempo de caminata
    Tpar<-c()

################################################################

    Tres<-c() #tiempo restante del recorrido en el día
            Vt<-sample(as.vector(Vtray), 1,replace =T) ##  extrayendo la
velocidad de trayectoria
            A<-sample(as.vector(Atray), 1,replace =T)     #extrayendo el
ángulo de la trayectoria
            Tca<-sample(as.vector(Tmov), 1,replace =T)    # Extrayendo el
tiempo de caminata
            Dis<-Vt*Tca          #calculando la distancia en función del
tiempo y la velocidad
            X1<-Xini+(sin(A)*Dis)  #generando las coordenadas en posición
final del desplazamiento
            Y1<-Yini+(cos(A)*Dis)
            Td<-Tca

    Per1<-Tca
    Tpar<-1#Tiempo de parada
    TDig<-0
    index<-c()

     i<-1
   Per<-Per1<Tsimul  # valor lógico de parada para el bucle que se genera
por día

     while(Per) # ciclo del día
        {

#Alimento
                TablaXY[i,2]<-X1
                TablaXY[i,3]<-Y1
                Tc<-sample(as.vector(Tfeed), 1,  replace =T)##extrayendo
el tiempo de comer
                Td<-Td+Tc    #estimando el tiempo del día que se ha
realizado
                Per1<-Per1+Tc


                                        Dseed<-sqrt((XYseed[,1]-
TablaXY[i,2])^2+(XYseed[,2]-TablaXY[i,3])^2) #valores menos las coord tabla
de semillas
                                          if(min(Dseed)>100){
                                            #SI HAY SALIDA DEL AREA DE
ESTUDIO
```

```
                                             X1<-
TablaXY[i,2]+(sin(A)*Dis)   #generando las coordenadas en posición final del
desplazamiento
                                             Y1<-
TablaXY[i,3]+(cos(A)*Dis)
                                             TablaXY[i,2]<-X1
                                             TablaXY[i,3]<-Y1
                                             Dseed<-sqrt((XYseed[,1]-
TablaXY[i,2])^2+(XYseed[,2]-TablaXY[i,3])^2) #valores menos las coord tabla
de semillas
                                                l<-XYseed[Dseed<=radio,3]
                                                 if(min(Dseed)>100){
                                    #SI  HAY  SALIDA  DEL  AREA  DE
ESTUDIO
                                             X1<-
TablaXY[i,2]+(sin(A)*Dis)   #generando las coordenadas en posición final del
desplazamiento
                                             Y1<-
TablaXY[i,3]+(cos(A)*Dis)
                                             TablaXY[i,2]<-X1
                                             TablaXY[i,3]<-Y1
                                             Dseed<-sqrt((XYseed[,1]-
TablaXY[i,2])^2+(XYseed[,2]-TablaXY[i,3])^2)#valores menos las coord tabla
de semillas
                                                l<-XYseed[Dseed<=radio,3]
                                                             }
                                              else {
                                             l<-XYseed[Dseed<=radio,3]
                                                    }
                                                        }
                                        l<-XYseed[Dseed<=radio,3]
#sacando el número de semillas en el radio indicado

                                     if(is.null(l1))
                                       {
                                              l1<-
sum(na.omit(l)/length(l)) #Sancando un valor promedio por si quedan varios
pixeles

                                        TDig<-
sample(as.vector(Tdig),1,replace =T) #condicionando si hay semillas para
estimar el tiempo de digestion
                                        Tpar<-Td+TDig
                                        index<-i
                                        TablaXY[i,1]<-index
                                        TablaXY[i,2]<-X1
                                        TablaXY[i,3]<-Y1
                                        TablaXY[i,4]<-l1
                                        TablaXY[i,5]<-TDig
                                        l<-c()
                                        }
                                    if(l1==0){l1<-c()}

                        if(!is.null(l1))
                        {
                         if(!is.na(l1))#  pregunta  si  el  tiempo  de
digestión es menor que el periodo del día
                                {
                            if((Tpar<Tday)){
```

```
                                                    #estimando   el   tiempo   de
digestión
                                    Tres<-TDig>1
                                    p<-i
                          while(Tres){
                                          Trest1<-
sample(as.vector(Trest),1,replace =T)
                                          Par<-c();        Td<-Td+Trest1;
Per1<-Per1+Trest1
                                          Par<-Tpar>Td
                                          if(Par){
                                                  TSeed[p,1]<-X1
                                                  TSeed[p,2]<-Y1
                                                  TSeed[p,3]<-
sqrt(((X1+(sin(A)*Dis))-TablaXY[index,2])^2+((Y1+(cos(A)*Dis))-
TablaXY[index,3])^2)
                                                  TSeed[p,4]<-
TablaXY[index,4]
                                                  TSeed[p,5]<-c('N')
                                                          l1<-c()
                                                          index=c()
                                                          Tpar<-c()
                                                          Tres<-
FALSE
                                              }
                                          else{Tca<-
sample(as.vector(Tmov), 1,replace =T)
                                              Td<-Td+Tca;        Par<-
Tpar>Td   ; Per1<-Per1+Tca
                                              Vt<-
sample(as.vector(Vtray), 1,replace =T)
                                              A<-
sample(as.vector(Atray), 1,replace =T)
                                              Dis<-Vt*Tca
                                              X1<-X1+sin(A)*Dis
                                              Y1<-Y1+cos(A)*Dis
                                              TablaXY[p,2]<-X1
                                              TablaXY[p,3]<-Y1
                                          if(Par){
                                              TSeed[p,1]<-X1
                                              TSeed[p,2]<-Y1
                                              TSeed[p,3]<-sqrt((X1-
TablaXY[index,2])^2+(Y1-TablaXY[index,3])^2)
                                              TSeed[p,4]<-
TablaXY[index,4]
                                              TSeed[p,5]<-c('N')
                                                          l1<-c()
                                                          index=c()
                                                          Tpar<-c()
                                                          Tres<-
FALSE
                                                }else            {Tc<-
sample(as.vector(Tfeed), 1, replace =T)
                                              Td<-Td+Tc
                                              Per1<-Per1+Td
                                              Par<-c()
                                              Par<-Tpar>Td
```

```
                                                          if(Par){
                                                          TSeed[p,1]<-X1
                                                          TSeed[p,2]<-Y1
                                                          TSeed[p,3]<-
sqrt((TSeed[p,1]-TablaXY[index,2])^2+(TSeed[p,2]-TablaXY[index,3])^2)
                                                          TSeed[p,4]<-
TablaXY[index,4]

                                                          TSeed[p,5]<-c('N')
                                                                    l1<-
c()

index=c()

                                                                    Tpar<-
c()
                                                                    Tres<-
FALSE
                                                          }

                                                     }
                                                   }
                                             p<-p+1
                                          }
                                       }
                                       }
                                       }

#####################################################################

## Preguntar si tiempo del día es mayor a 720 que duerma marque si hay
semillas o que luego siga
       if(Td>Tday)
                {
                Per1<-Per1+Tnight
             if(!is.null(l1))
              {Tpar<-abs(Tpar-Tnight)
            if(Tpar<Tnight){
                 if(!is.na(l1)) {
                                TSeed[i,1]<-X1
                                TSeed[i,2]<-Y1
                                TSeed[i,3]<-sqrt((TSeed[i,1]-
TablaXY[index,2])^2+(TSeed[i,2]-TablaXY[index,3])^2)
                                TSeed[i,4]<-l1
                                TSeed[i,5]<-c('S')
                                Td<-1
                                index<-c()
                                Tpar<-c()
                                l1<-c()
                                  }
                 }
             else {Tpar<-Tpar
                 Td<-1
                       }
                  }
                Td<-1
                }

Trest1<-sample(as.vector(Trest),1,replace =T)#descansa
Td<-Td+Trest1 ; Per1<-Per1+Trest1
```

```
## Preguntar si tiempo del día es mayor a 720 que duerma marque si hay
semillas o que luego siga
      if(Td>Tday)
                {
                Per1<-Per1+Tnight
            if(!is.null(l1))
             {Tpar<-abs(Tpar-Tnight)
            if(Tpar<Tnight){
                if(!is.na(l1)) {
                             TSeed[i,1]<-X1
                             TSeed[i,2]<-Y1
                             TSeed[i,3]<-sqrt((TSeed[i,1]-
TablaXY[index,2])^2+(TSeed[i,2]-TablaXY[index,3])^2)
                             TSeed[i,4]<-TablaXY[index,4]
                             TSeed[i,5]<-c('S')
                             Td<-1
                             index<-c()
                             Tpar<-c()
                             l1<-c()
                                 }
            }
              else {Tpar<-Tpar; Td<-1}
              }
               Td<-1
              }

      Tca<-sample(as.vector(Tmov), 1,replace =T) #Camina
      Td<-Td+Tca; Per1<-Per1+Tca
      Vt<-sample(as.vector(Vtray), 1,replace =T)
      A<-sample(as.vector(Atray), 1,replace =T)
      Dis<-Vt*Tca
      X1<-TablaXY[i,2]+sin(A)*Dis
      Y1<-TablaXY[i,3]+cos(A)*Dis

## Preguntar si tiempo del da es mayor a 720 que duerma marque si hay
semillas o que luego siga
      if(Td>Tday)
                {
                Per1<-Per1+Tnight
            if(!is.null(l1))
             {Tpar<-abs(Tpar-Tnight)
            if(Tpar<Tnight){
                if(!is.na(l1)) {
                             TSeed[i,1]<-X1
                             TSeed[i,2]<-Y1
                             TSeed[i,3]<-sqrt((TSeed[i,1]-
TablaXY[index,2])^2+(TSeed[i,2]-TablaXY[index,3])^2)
                             TSeed[i,4]<-l1
                             TSeed[i,5]<-c('S')
                             Td<-1
                             index<-c()
                             Tpar<-c()
                             l1<-c()
                                 }

            }
            else {Tpar<-Tpar; Td}
            }
                Td<-1
```

```
                  }

i<-i+1
Per<-Tsimul>Per1
          }
#Distmax[j,1]<-j
#Distmax[j,2]<-max(na.omit(TSeed)$DistExc)

BW[j,1]<-j

if(length(na.omit(TSeed)$DistExc)>3){
BW[j,2]<-density((na.omit(TSeed)$DistExc),      bw="ucv",      width      =
length((na.omit(TSeed)$DistExc)), window = "gaussian")$bw
                                     }

TablaG[[j]]<-na.omit(TSeed)
TablaG1[j,1]<-j
TablaG1[j,2]<-length(na.omit(TSeed)[,3])

########################################################################
 }
Tabla<-do.call(rbind, TablaG)
SS=summary(subset(Tabla,Letrinas=='S')$DistExc)
SN=summary(subset(Tabla,Letrinas=='N')$DistExc)
ST=summary(Tabla$DistExc)
SUMAR=rbind(SN,SS,ST)
colnames(SUMAR)<-names(ST)
Frec=table(Tabla$Letrinas)
Frec.L=cbind(Frec)
Frec.L1=rbind(Frec.L,length(Tabla$DistExc))
Summary.<-data.frame(c('No latrine','Latrine',  'Total'), SUMAR, Frec.L1)
colnames(Summary.)<-c('Variable','Min.','1st       Qu.','Median','Mean','3rd
Qu.','Max.', 'Frequency' )


Resultados<-list(Summary.,TablaG,BW, TablaG1)
names(Resultados)<-c('Summary','dist_exc','ECM','Frequency runs')
save(Resultados, file = file)
}
```

```
# MODEL OUTPUTS

Output<-Traj_monkeys(XYini, Vtray,Atray, Tmov, Tfeed, Trest,Tdig, XYseed,
It, Tsimul,radio, Tday, Tnight, directory, file)
```