Do Megafauna influence spatial patterns of nutrient distribution?
An empirical study of litter and soil mineral concentrations at the Langoué Bai, Gabon.

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Abstract

Forest elephants are the largest forest-dwelling animals, and the dominant herbivores structuring the forests of Central Africa. Illegal ivory poaching threatens these animals with extinction, so it is important to understand their function in the ecosystem and the potential consequences of their removal. A recently developed theoretical model suggests that elephants may play a disproportional role in nutrient diffusion from areas of high to low fertility. This study is the first empirical attempt to test the predictions generated by this model. I analysed the spatial patterns of nutrient concentration in soil and litter samples at the Langoué Bai in Gabon. I identified only limited support for the hypotheses of animal mediated dispersal away from the bai, and that elephant paths may act as "nutrient arteries" in the system. Further study of this system is required to fully understand the role of the bai, and of elephants as dispersers of nutrients.

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1. Introduction

Large animals – known collectively as megafauna – are often important ecosystem engineers. In modern day Central Africa, the largest animal is the forest elephant, *Loxdonta africana cyclotis*. These are under increasing pressure from poaching for ivory, and face the possibility of extinction from the wild in the present century. In this thesis, I review the status, behaviour, and ecological significance of forest elephants and explore the possible ecological consequences of their removal by drawing insight from the Pleistocene megafaunal extinctions. There is a wealth of literature documenting the role of elephants as dispersers of seeds, but recent attention also suggests an important role in nutrient cycling and mineral dispersal. I then contribute to this emerging body of knowledge by presenting an empirical study of litter and soil mineral concentrations in the area around an important forest elephant aggregation site – the Langoue Bai at Ivindo National Park, Gabon.

1.1. Taxonomy and conservation status of African forest elephant

The African elephant *Loxodonta africana* currently consists of two extant subspecies; the savannah or bush elephant *Loxodonta africana africana;* and the forest elephant *Loxodonta africana cyclotis.* These differ in behaviour and ecology, and accumulating morphological (Grubb, Groves, Dudley, J, & Shoshani, 2000) and genetic (Brandt, Ishida, Georgiadis, & Roca, 2012; Ishida et al., 2011; Roca, Georgiadis, & O'Brien, 2007; Rohland et al., 2010) data strongly suggest that they function as distinct species. The forest elephant population is largely confined to the equatorial forests of Central Africa, with about 5% of 'known' and 'possible' range occurring in West Africa, to the West of Cameroon-Nigeria border (Maisels et al., 2013).

African elephant populations have been decimated by waves of hunting for ivory at several points in history. Ivory hunters lead to local extirpations of (mainly savannah) elephants in North Africa in the early middle ages, South Africa in the eighteenth and nineteenth century, West Africa in the late nineteenth and early twentieth century, and Northern Somalia in 1950's (Douglas-Hamilton, 1979). An estimated increase in the volume of ivory extracted during the second half of nineteenth century is attributed to rapidly increasing prosperity in Europe at the time, which pushed up the demand and price for ivory as a luxury item (Barnes, 1996). Most of the ivory from the nineteenth century onwards has likely come from forest elephants (Douglas-Hamilton, 1979). Volumes of ivory exports recorded from central Africa

appear to have largely subsided for decades following 1914, likely due to a combination of population declines, poorer record keeping (disrupted by war), and introduction of conservation regulations by colonial governments (Barnes, 1996; Douglas-Hamilton, 1979). However, another upsurge of ivory trade across the continent was observed during the 1970s and 1980s, in response to increasing wealth and demand for ivory in East Asian countries, and facilitated by the spread of automatic weapons (Barnes, 1996; Douglas-Hamilton, 1983).

In 1989, ivory trading was formally banned by the Convention on International Trade in Endangered Species (CITES). This was followed by localised recoveries in elephant populations during the 1990's particularly in southern African countries, but as Ginsberg (2002) pointed out, neither the ban nor the follow-up enforcement activities were structured in a way that would answer whether the population recoveries were related to a decline in demand or improved enforcement of anti-poaching laws. The respite was brief and despite the on-going ban on ivory trade, the illegal trade has dramatically escalated since the turn of the century. A recent study reports a catastrophic decline of forest elephant between 2002 and 2011 — a loss of ca. 62% of the population in Central Africa, and a 30% reduction in geographical range (Maisels et al., 2013). The remaining population is reported to be now less than 10% of its potential size, and occupying less than 25% of its potential range.

The illegal commerce in ivory shows no signs of abating, sustained by demand from the emerging middle classes in East Asia, particularly in China and Vietnam (Vigne & Martin, 2011). This demand is coupled with widespread corruption and political instability in several key countries, and with the rapid expansion of roads for logging and development into increasingly more remote areas, which facilitate the access of poachers to elephants (Blake et al., 2008; Maisels et al., 2013). As a result, the distribution of modern elephant populations is governed more by human factors than it is by environmental ones (de Boer et al., 2013), as is illustrated by the mirrored pattern of forest elephant density and the frequency of human signs in a major national park in the Congo Basin (Figure1) (Blake et al., 2007). If elephant poaching and the demand for elephant ivory and are not drastically curbed soon, forest elephants face a real threat of extinction from the wild in the near future (Maisels et al., 2013).
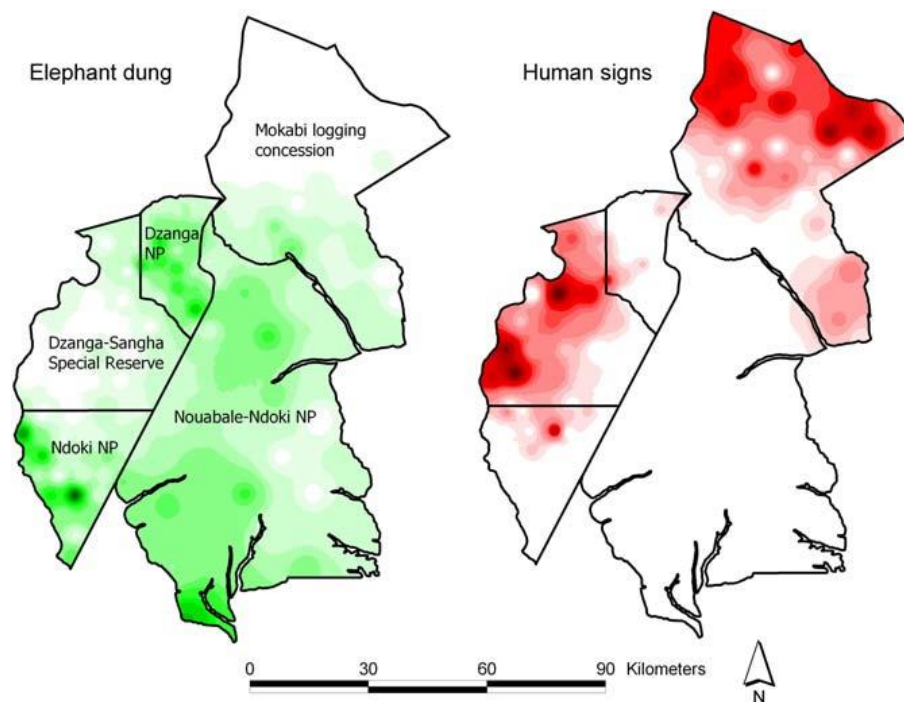
Figure 1. Interpolated Elephant Dung Count and Human-Sign Frequency accros the Ndoki-Dzanga conservation area. Increasing colour intensity represents increasing frequency of dung(green) and human signs (red). Source: (Blake et al., 2007)

1.2. Forest elephant behaviour and ecology

Closed-canopy forest habitat and secretive habits mean that direct observation of forest elephant behaviour is difficult, and available data remains sparse (Schuttler, Blake, & Eggert, 2012). Observations at forest clearings ("bais") suggest that forest elephants form fission-fusion societies similar to those described for African savannah elephants (Fishlock & Lee, 2013). This means that basic family units form larger groups, often of related individuals, whose size fluctuates and that associate and dissociate through time. Individuals form lasting relationships not only with members of their own basic family unit, but also with members of other such groups.

The family units of savannah elephants usually comprise two or more related adult females and their offspring, often aggregating into groups of dozens of individuals. For forest elephants, however, a unit is usually only a single female with offspring, with mean group size of around three individuals (Merz, 1981; White, Tutin, & Fernandez, 1993). Adult bulls of forest elephant are solitary (Morgan & Lee, 2007; Turkalo & Fay, 2001). Although forest family units forage separately, it is suggested that, similarly to savannah elephants, related families coordinate their movements through the forest via the use of infrasonic sounds (Poole, Payne, Langbauer Jr, & Moss, 1988; White et al., 1993). Gatherings of large numbers

at forest clearings are common, reaching in excess of one hundred individuals at the same time (Turkalo & Fay, 2001). The clearings likely play a special role as arenas for social interactions between different groups, providing opportunities to establish and reinforce social hierarchy, and to strengthen family ties (Fishlock & Lee, 2013; Turkalo & Fay, 2001).

In contrast to savannah elephants, whose diet is in 90% composed of herbaceous plants, forest elephants feed mainly on the leaves and fruits of trees, although they eat a variety of herbaceous plants as well (Blake, 2002; Morgan & Lee, 2007). It has been hypothesised that the smaller group size of forest elephants is related to their frugivory, as ripe fruits are a patchily available resource that may be exploited more efficiently by smaller rather than larger groups (White et al., 1993). Seasonal movements of forest elephants appear strongly influenced by fruiting patterns (Lee J. T. White, 1994).

Equatorial forests of Central Africa generally grow on very nutrient-poor soils, and elephants may need to supplement their diets with salts (particularly sodium) from other sources to meet their nutritional requirements. Forest elephants are found to regularly visit coastal habitat if they have access to it, likely in order to increase sodium intake through the consumption of salt-coated vegetation (Morgan & Lee, 2007). In savannah elephants, geophagy (soil eating) at salt licks and termite mounds, as well as crop raiding, and preference for browse on termite mounds (which has higher mineral concentrations than browse away from mounds) have all been associated with nutritional deficiency, particularly in sodium (Holdø, Dudley, & Mcdowell, 2002; Holdo & McDowell, 2004; Rode, Chiyo, Chapman, & McDowell, 2006; Ruggiero & Fay, 1994). In forests, localised deposits of higher concentrations of sodium and other cations become focal sites for fauna, and elephants often forage directly on soil at such places.

Bais - forest clearings, generally located on a watercourse (Momont, 2007; Turkalo & Fay, 2001) – can be indicative of important mineral deposits. For example, those studied in the Hokou area of the Dzanga-Sangha National Park, Central African Republic, were shown to be located on dolerite rock intrusions, and contained soils much enriched in clay and cations such as potassium, sodium, magnesium, and calcium, compared to forest soils found one or four kilometres away (Klaus, Klaus-Hugi, & Schmid, 1998). Elephants dig holes in such areas (presumably) to extract the soil from mineral-rich layer, either directly by eating it or drinking mineral-enriched water. Large bais attract large numbers of elephants, for example, over 1000 individuals are known to visit the Langoué Bai in Ivindo National Park in Gabon

(Momont, 2007), and over 3000 individuals were recorded visiting Dzanga Bai in Dzanga-Sangha NP (Turkalo & Fay, 2001). These numbers much exceed the population size estimates based on dung counts and density estimates in the surrounding forests, indicating that elephants travel to these bais from large distances (Turkalo & Fay, 2001).

The distribution of elephant trails in the forest has been shown to be influenced by the location of mineral deposits and fruiting trees, and appears designed to maximise the efficiency of movement between areas of interest (Blake & Inkamba-nkulu, 2004; Vanleeuwe & Gautier-hion, 1998). Trail systems seem to be semi-permanent, and several types are recognised, including: 'boulevards' used for fast directional travel, often over large distances; 'foraging trails', which are shorter and more sinuous; and 'clearing alleys' forming a dense network of trails surrounding most forest clearings (Vanleeuwe & Gautier-hion, 1998).

Besides building large networks of forest paths, elephants contribute to habitat diversity by maintaining canopy gaps and forest clearings through trampling and grazing plants. This helps to maintain the availability of light-loving herbaceous plants, especially from the *Marantaceae* and *Zingiberaceae* families, which are an important food source for elephants and great apes (L J T White et al., 1993). They also frequently trample and uproot small and medium size trees, which may reduce the root competition for large trees, and promote their longevity. This in turn may increase biomass and the carbon storage capacity in the forest, as large trees store proportionally more carbon (Lewis et al., 2013) (Slik et al., 2013).

1.3. Elephants as dispersers of seed

Dispersal is a key processes in plant communities, critical for colonising suitable habitat and for maintaining gene flow between populations, thus enhancing population genetic diversity and resilience to environmental change (Ouborg, Piquot, & Van Groenendael, 1999). The distance that seed is dispersed is especially important (Blake, Deem, Mossimbo, Maisels, & Walsh, 2009), with long distance dispersal potentially allowing for the establishment of poorer competitor species simply because superior competitor seeds fail to arrive. Also, moderate to long dispersal may be important for escaping Janzen-Connell effects (Connell, 1971; Janzen, 1970), i.e. density-dependent effects of pathogen infections, seed predation and kin/sibling competition. Thus, species able to effectively disperse over long distance may have a comparative advantage over less-able species (Nathan & Muller-Landau, 2000).

Frugivorous animals provide an effective means of dispersal and many tropical plant species evolved mutualistic relationships with vertebrate frugivores for this purpose.

Large frugivores are superior dispersers compared to smaller-sized frugivores: higher number of seeds consumed per individual as well as higher ranging ability and long gut passage times allow a large number of seeds to be transported over long distances, and overcome Janzen-Connell effects (Blake et al., 2009; Guimarães, Galetti, & Jordano, 2008). Moreover, bigger ranges provide large herbivores access to a higher number of trees, so they consume and disperse a greater number and diversity of seeds than small dispersers do (A. L. M. Curran & Leighton, 2000; L. Curran & Webb, 2000). Large herbivores are also likely to be more efficient consumers, thanks to larger brain size and superior ability to remember the location and phenology patterns of fruiting trees (Mace, Harvey, & Clutton-Brock, 1980). Unsurprisingly, many tropical trees evolved mutualistic relationships with the largest frugivores in their ecosystems. In African forests this is, of course, the elephant.

Elephants were found to disperse seeds of more species than any other animal genus in the Congo basin, and also to disperse them far more widely than any other animal vector (Blake et al., 2009). Forest elephants are documented to disperse seeds from over a hundred different species at a single site (i.e. a single studied forest), with an average of 43 plant species dispersed per site (Campos-arceiz & Blake, 2011; Poulsen, Clark, & Smith, 2001). The majority of these are trees (average of 39 tree species dispersed per site).

Large seeds, typical of trees, take 72 h or longer to pass through the gut of a forest elephant, and can regularly be moved over 5km away from the parent tree (Blake et al., 2009). The maximum dispersal distance recorded for a forest elephant was 57km in 72h, which encompasses several times the home range even of the next biggest frugivore in the forest (the gorilla), and dwarfs the dispersal distances of other species including apes, monkeys, or hornbills (Blake et al., 2009).

Although obligate dispersal relationships — where a plant relies exclusively on a single animal species for dispersal — are rather exceptional, they seem to have evolved for a number of tree species dispersed by elephants (Campos-arceiz & Blake, 2011). Often referred to as species with "megafaunal syndrome", or simply "megafaunal species", they produce fruits with similar characteristics. Such fruits tend to be large, dense and fleshy, inconspicuously coloured (elephants are mostly colour blind), and release a strong smell

(Guimarães et al., 2008). At Ndoki forest in Republic of Congo, thirteen tree species display the megafaunal syndrome. At landscape scale (up to 67km linear distance) these species were found to be distributed essentially randomly, whilst the similarity of species with other dispersal syndromes — non-obligate elephant dispersal, other-animal dispersal, wind dispersal, and dispersal by gravity — decayed with increasing distances, mostly in this order (Blake et al., 2009). Other elephant-dispersed but non-obligate trees were also less aggregated than species in the remaining functional guilds, even though fruit–fall was strongly clustered around mother trees. This is suggestive of strong Janzen-Connell effects on juvenile tree mortality and implies that elephants enhance recruitment in all species whose seeds they disperse (Blake et al., 2009).

Given their clearly important role in seed dispersal, what might be the repercussions for the Central African forests if elephants were to disappear – an all-too-real possibility? Part of the answer to this question may be gleaned from studies on the ecological effects of Pleistocene megafaunal extinctions.

Between some 50,000-10,000 years ago, in the late Pleistocene, 97 genera of megafauna (large mammals >44kg) went extinct (Barnosky et al., 2004). The causes of these extinctions are much debated, and are variably attributed to overkill by early humans colonising new lands, or climate change and resulting vegetation change. It is possible that these influences were synergistic, with extinctions resulting from the hunting pressure by humans compounded by additional environmental changes. Crucially, in many cases the Pleistocene megafaunal extinctions predated, rather than followed changes in vegetation communities, implying that the loss of largest herbivores was a driver, rather than a consequence, of changes in vegetation (Gill, Williams, Jackson, Lininger, & Robinson, 2009; Johnson, 2009).

In tropical rain forests, possibly the largest influence of the Pleistocene mega herbivore extinction was the consequential loss of their mutualistic interactions from the ecosystem, leaving the co-adapted plants with anachronisms in the form of obsolete defence systems and, in the case of megafaunal species, dysfunctional dispersal mechanisms (Guimarães et al., 2008). Based on the trait profile of African species currently disperserd by elephants, Guimarães *et al.* (2008) identified 103 species with megafaunal syndrome living in Brazil. These were presumably once dispersed by the now-extinct gomphotheres (forest-dwelling relatives of elephants), and nowadays have mostly restricted distributions and genetic signatures reflective of isolated populations. Many more such species have likely already

gone extinct (Johnson, 2009). Similar observations on various continents suggest that "in many parts of the world, vegetation communities are in various stages in a process of long-term relaxation from a megafauna-conditioned to a megafauna-naive state, due to initial decline and ultimate extinction of plants that had formerly interacted strongly with extinct large herbivores" (Johnson, 2009, p.2516).

A recent study in the Salonga National Park in Democratic Republic of Congo provides evidence that the same process has already began in those Central African forests where elephants were extirpated (Beaune, Fruth, & Bollache, 2013). Due to human activities, elephants in Salonga NP have been functionally extinct for several decades (i.e. persist only at numbers too low to significantly interact with their ecosystem). Out of the eighteen obligate megafaunal tree species identified in the Park, twelve failed to recruit completely (the youngest cohorts were absent), two were recruiting at levels too low for self-replacement, and for the remaining species the spatial structures of the young cohorts were more clumped than for the adults, but did not differ for control (non-megafaunal) species (Beaune, Fruth, et al., 2013).

The majority (over 95% in some forests) of trees in Central African forests depend on animals for dispersal (Beaune, Bretagnolle, et al., 2013), and the current presence of elephants may tip the competitive balance towards the species-rich guild of large woody trees with big fruits (Blake et al., 2009; Campos-arceiz & Blake, 2011). The disappearance of elephants and progressive defaunation of the forests might reverse this balance and open a "new era" for the wind and ballistic dispersed species (Beaune, Bretagnolle, et al., 2013). Such species tend to be fast-growing and have low-wood density, and their dominance may diminish the long-term potential for carbon storage (Poulsen, Clark, & Palmer, 2013). Considering that tropical forests are responsible for about a third of global terrestrial metabolic activity and that the forest block in the Congo Basin is the second largest tropical forest in the world, the defaunation of Central Africa might have significantly reduce the size of current carbon sink in tropical forests (Malhi, 2012; Poulsen et al., 2013).

1.4. Elephants as dispersers of nutrients?

Nutrient cycling

Nutrient availability is critically important to ecosystem structure and function. It has a strong impact on primary productivity (Cleveland et al., 2011; Menge, Pacala, & Hedin, 2009; P. M.

Vitousek & Sanford, 1986; P. Vitousek, 1984), tree species distribution (Fyllas et al., 2009) and animal biomass and distribution (Asner & Levick, 2012; S. J. McNaughton, Banyikwa, & McNaughton, 1997). In forests, plant growth rate is often nutrient-limited (P. M. Vitousek & Sanford, 1986).

In tropical rain forests, abiotic factors affecting nutrient cycles and availability, such as hydrological cycles (Bruijnzeel, 2009; Clark, Nadkarni, Schaefer, & Gholz, 1998; P. M. Vitousek & Sanford, 1986), deposition of river sediment (Dezzeo, Herrera, Escalante, & Chacón, 2000), and dry atmospheric deposition (Pett-Ridge, 2009) have been relatively well studied. Equally, the contribution of microbial and invertebrate decomposers has been addressed (Cleveland, Reed, & Townsend, 2006; González & Seastedt, 2001; Heneghan, Coleman, & Zou, 1999). By contrast, very few studies to date focused on the impacts that vertebrates may have on nutrient budgets and cycling in tropical rain forests (but see Bluethgen, Schmit-Neurburg, Engwald, & Barthlott, 2001; Feeley & Terborgh, 2005; Stevenson & Guzmán-Caro, 2010).

Vertebrate herbivores can influence various components of nutrient cycling, including the relative size of nutrient pools in soil, litter, and biomass; the rates of nutrient fluxes including litter–fall, decomposition, mineralisation, and plant uptake; and nutrient fluxes in and out of the ecosystem including volitisation, denitrification, leaching, and lateral nutrient transport due to animals emigrating and immigrating into the ecosystem (Feeley & Terborgh, 2005; Singer & Schoenecker, 2003). These influences may both enhance, or suppress nutrient cycling. For example, vegetation trampling and fertilization through faeces and urine deposition may increase decomposition and uptake rates, and grazing may elicit a compensatory response that stimulates plant growth (S. McNaughton, 1976; Seagle, McNaughton, & Ruess, 1992; Singer & Schoenecker, 2003), whilst altering vegetation communities towards less palpable and more slowly decomposing species can decrease cycling rates (de Mazancourt C & Loreau, 2000; Singer & Schoenecker, 2003). These insights, however, come mostly from studies of grassland systems, and our understanding of the effect that herbivores may have on nutrient cycling and availability within tropical forests remains very limited (Feeley & Terborgh, 2005; Stevenson & Guzmán-Caro, 2010).

Lateral nutrient transport

A number of papers document vertebrates as vectors for nutrients crossing the boundary between water and terrestrial realms. For example, moose *Alces alces* at Isle Royale National Park in USA have been shown to feed primarily on mycrophyte vegetation in freshwater habitats, but to excrete and die primarily on land, creating a significant Nitrogen flux into the riparian zone (Bump, Tischler, Schrank, Peterson, & Vucetich, 2009). In the Kenai Peninsula in Alaska, about 16% of foliar Nitrogen in spruce within the riparian zone has been shown to be the δ^{15} Nitrogen stable isotope derived from salmon, and brought onto land by brown bears *Ursus arctos* fishing in the streams (Hilderbrand, Hanley, Robbins, Charles, & Schwartz, 1999). The δ^{15} N stable isotope signature in leaves was highly correlated with locations of radio-collared brown bears relative to distance from streams, and declined rapidly after the distance of 500 meters.

The fluxes are also possible in the opposite direction. For instance, through daily foraging trips to the surrounding fields, snow geese may supply 40% of N input and 75% of P input to their wintering grounds in the wetlands in the Apache Reserve, New Mexico (Kitchell et al., 1999).

In probably the only study to date on animal-mediated nutrient transport in tropical rain forests, a population of woolly monkeys has been shown to transport nitrogen, phosphorous, and potassium in the form of seeds, within and between *terra firme* and flooded forests (Stevenson & Guzmán-Caro, 2010). Quantities of phosphorous transported were comparable in magnitude to abiotic inputs to the system, although relative inputs of the other minerals were low. Translocation to the *terra firme* forest from the flooded forest amounted to approximately 25% of the total nutrients transported by monkeys, and that from *terra firme* forest to flooded forest for approximately 5%. Since the flooded forests are higher in nutrients than the *terra firme* forests, nutrient translocation by monkeys from flooded to *terra firme* forest may constitutes a small yet important nutrient flux. It is particularly noteworthy since it operates in the opposite direction to abiotic processes governing fluxes in this environment, such as leaching and runoff, which tend to move the biomass from the nutrient-poor and concentrate them in nutrient-rich sites.

Whilst these studies highlight the potential for animal mediated lateral nutrient transport, overall, the literature remains relatively meagre, and most papers present case studies focusing on single species, the amount of nutrients transported, and their assimilation in the ecosystems. Much less attention has been paid to the spatial patterns of lateral nutrient transport by animals, or to the effects that whole animal communities may exert of ecosystem function through this process. Yet whole-system level perspective of this process is important, not only to understand ecosystem function within an ecosystem, but also the higher-level "meta-ecosystem" properties that arise from spatial fluxes of nutrients, energy, and individuals coupling separate ecosystems at different scales, including at regional and continental scale (Polis, Anderson, & Holt, 1997)(Loreau, Mouquet, & Holt, 2003).

Mathematical model of nutrient transport by animals

Recently, a mathematical framework has been developed to predict the spatial patterns of lateral nutrient transport in terrestrial systems mediated by mammalian herbivores. The model describes the dispersal of nutrients by animals as a diffusion-like process, from high– to low– concentration areas. No individual animal is thought to move through the landscape randomly, however, the use of diffusion process in the model is justified based on the assumption that, over the long geological timescales relevant to biogeochemical process, the location of the sites of interest to animals such as foraging hotspots, wallows etc., is not permanent, and aggregated movements of the whole animal community can be approximated as random.

The equation describing the dynamic probability density function of the nutrient P, as governed by a random walk of length Δx over time Δt is:

$$\frac{\partial P}{\partial t} = \Phi_{excreta} \frac{\partial^2 P}{\partial x^2} + \Phi_{body} \frac{\partial^2 P}{\partial x^2}$$

where Φ denotes a constant of proportionality called "diffusivity", which is determined by the availability of edible biomass (per $km^{2)}$), animal consumption rate, animal population density, time from nutrient particle ingestion to its release, and animal displacement over this time (see equation (3) and (4) in Wolf, Doughty, & Malhi, 2013). The diffusivity for the nutrients transported through excretions ($\Phi_{excreta}$) differs from the diffusivity for nutrients incorporated into animal body mass (Φ_{body}), since the time and spatial scale relevant for the

former are determined by gut passage time and daily displacement, whilst for the latter the timescale approximates animal lifetime, and the length is determined by home range .

All factors determining Φ, except for the availability of edible biomass, have significant scaling relationships with animal body size, which means Φ can be approximated even for animals for which no behavioural data is available, based only on their body size. An analysis of this equation for nearly 5300 terrestrial mammal species revealed that Φ_{body} is four orders of magnitude smaller than $\Phi_{exrecta}$ and may therefore be safely ignored in calculations of nutrient fluxes. Moreover, the results highlighted the disproportional contribution of large-bodied species to nutrient dispersal, mostly due to their longer gut passage times and higher daily ranges (*ibid*).

The authors conclude that that this function has already been substantially reduced due to Pleistocene megafaunal extinctions, leading some regions of the world such as the Amazon basin to become oligotrophic. In Central Africa however, megafauna such as elephants may still be fulfilling this function. On-going defaunation and the possible extirpation of elephants in particular, may impact the Central African ecosystem not only through changes in seed dispersal and tree recruitment, but also through reducing nutrient fluxes, e.g. from alluvial forests, and thereby reducing soil fertility, primary productivity, and decomposition.

1.5. Introduction to the Present Study

The Wolf et al. (2013) model of lateral nutrient diffusion by mammalian herbivores (referred to from hereon as the Lateral Diffusion Model) provides a basis for predicting spatial patterns of animal-mediated nutrient fluxes. It is concerned with patterns on regional and continental spatial scales, and nutrient budgets of entire ecosystems, whose turnover rates are governed by biogeochemical cycles and vary between centuries and millennia (Menge et al., 2009). As such, any patterns of directionality in animal movements are expected to even out, and are approximated as essentially random. Where substantial gradients in nutrient concentrations exist − e.g. between habitats with differing bedrock or hydrological conditions − the model predicts an animal mediated diffusion like gradient from areas of high to areas of low concentration.

In this study, I make the first attempt to test the hypotheses generated under the Lateral Diffusion Model of Wolf et al. (2013). I make use of a naturally occurring nutrient hotspot – the Langoué Bai in Gabon - located in an area that boasts a relatively intact megafauna community – principally the African forest elephant. As previously described (see section 1.2.), bais are thought to provide forest mammals with a rich source of salts, including K, Ca, Mg and Na. The first three of these nutrients are also essential for plant growth, whilst Na enhances litter decomposition rates (Subbarao, Ito, Berry, & Wheeler, 2003). The study considered the mineral concentrations in specific pools (litter and soil), where in tropical forests, nutrients cycle on the scale of a few weeks to about four years (Menge et al., 2009; Schreeg, Mack, & Turner, 2013; Cleveland et al., 2006).

A principal objective of the study was the test the hypothesis:

> (i) That salts decrease in concentration with an increasing distance from the bai. I predicted to reveal either a logarithmic decline in concentration, that would be consistent with the hypothesis of animal-mediated dispersal, or a step-change, indicating very limited nutrient dispersal.

The focal sites of elephant activity — fruiting trees, and, especially mineral deposits — are likely to stay in one place over many generations, and thus the system of connecting boulevard trails is likely to be at least semi-permanent (Blake & Inkamba-nkulu, 2004). While the dynamics of the location of individual trails may be approximated as random at larger geographic and time scales, at smaller scales the non-random movement of herbivores along semi-permanent trails may result in trail-associated patterns of nutrient deposition. Therefore, further to considering the effect of distance from bai (hypothesis i), I also considered the following novel hypothesis:

> (ii) That salts decrease in concentration away from a main trail. This hypothesis is not mutually exclusive with hypothesis (i), but if supported, would indicate that elephant trails act as "nutrient arteries" within the forest landscape.

2. Methods

2.1. Study site

The study was conducted at the Langoué Bai in Ivindo National Park, Gabon between the 17th and the 27th of June 2013. This is the largest bai in Gabon, and the surrounding forest supports a relatively intact forest elephant population, unlike most other bais in the region where poaching is prevalent. The bai attracts over 1000 individual elephants, many of whom must travel tens of kilometres from their foraging ranges to reach it (Momont, 2007). Behavioural observations from the viewing platforms indicate that elephants spend most of their time at bai standing in water–filled holes and blowing air into the water before drinking (fig.2), a behaviour that is thought to increase the dissolved mineral content of the water (Momont, 2007). Visits during the day last about two hours (although likely longer at night), and over half of the time is spent using water holes. Much time may also be spent waiting to use a water hole if it is being occupied by an individual superior in hierarchy. These behaviours suggest that the bai is rich in minerals, and is an important resource for elephants (Momont, 2007).

Figure 2. Showing: a group of elephants using water holes the main site in the bai (left); an elephant splashing water as he pumps air into the water hole with his trunk. Photo credit: author

Ivindo National Park lies between 12°20 E– 12°59E, and between 0°21 N–0°17 S. Langoué Bai is located in the Southern part of the park (see fig. 3). The bai covers an area of 13.3ha, with a length of 850m and a width of between 100 and 350 meters (Vande weghe, 2009). It

is situated on a river valley on a North-South axis (see fig. 3, top image). On the West side, where most research has taken place, the bai is surrounded by about 15-20m wide belt of hydromorphic soils and low-lying forest, and then the terrain rises sharply to form a *terra firme* forested plateau.

The vegetation of Langoué Basin is intermediate between the Atlantic coastal forest of Lower Guinea, and semi-deciduous forest typical of central Congo Basin (Vande weghe, 2009). Mean annual precipitation is 1751 ± 199 mm and mean monthly temperature is 23.3±0.5°C (Momont, 2007). The general soil type, as indicated by regional-scale data, is that of highly acidic xanthic ferralsols – highly weathered, very nutrient-poor red soils, characteristic of many humid tropics (Jones et al., 2013).

There are four seasons in the year based primarily on precipitation: a short dry season from January to mid-February; a first rainy season from mid-February until the end of May; a long dry season from June to mid-September; and a second rainy season from mid-September to the end of December (Momont, 2007).

2.2. Study trails and transects

Three principal trails straddling the plateau to the West of the Langoué Bai were identified based on the expert knowledge of the Gabonese Wildlife Conservation Society (WCS) research assistants. These can be classified as local or within-zone boulevards, that are distinct from other trails in the area in that they remain in frequent use throughout the year. The within-zone boulevards originating near the Bai are likely to connect sites of interest to elephants within the Langoué area, including fruiting trees and mineral deposits on river beaches and in small salines distributed around the forests. Of these three boulevards, the one that was most easily accessible from the base camp was chosen for the study and it will hereafter be referred to as the 'main trial'.

The main trail enters the forest near the platform in the northern part of the bai (fig.4) and leads Northwest of the bai over the plateau, terminating at a crossing with a forestry road that leads to Ivindo (not shown on the map). The research base camp is located near the main trail, about halfway from the bai to the forestry road. The Eastern part of the main trail is used by WCS research assistants to access the bai, and the Western part is used to access the forestry road. Despite the presence of humans, the trail remains in constant use by elephants,

particularly during the first rainy season when they use it daily to travel between the bai and fruiting trees.

Figure 3. Showing: the location of national parks in Gabon (top left); the Ivindo National Park (top right); and the situation of the Langoué Bai (bottom left and right). The 'main site' of elephant watering holes, and the WCS elephant monitoring platforms are indicated in the bottom right panel. Source: Wikipedia Commons (top left), and Momont (2007) for remaining images
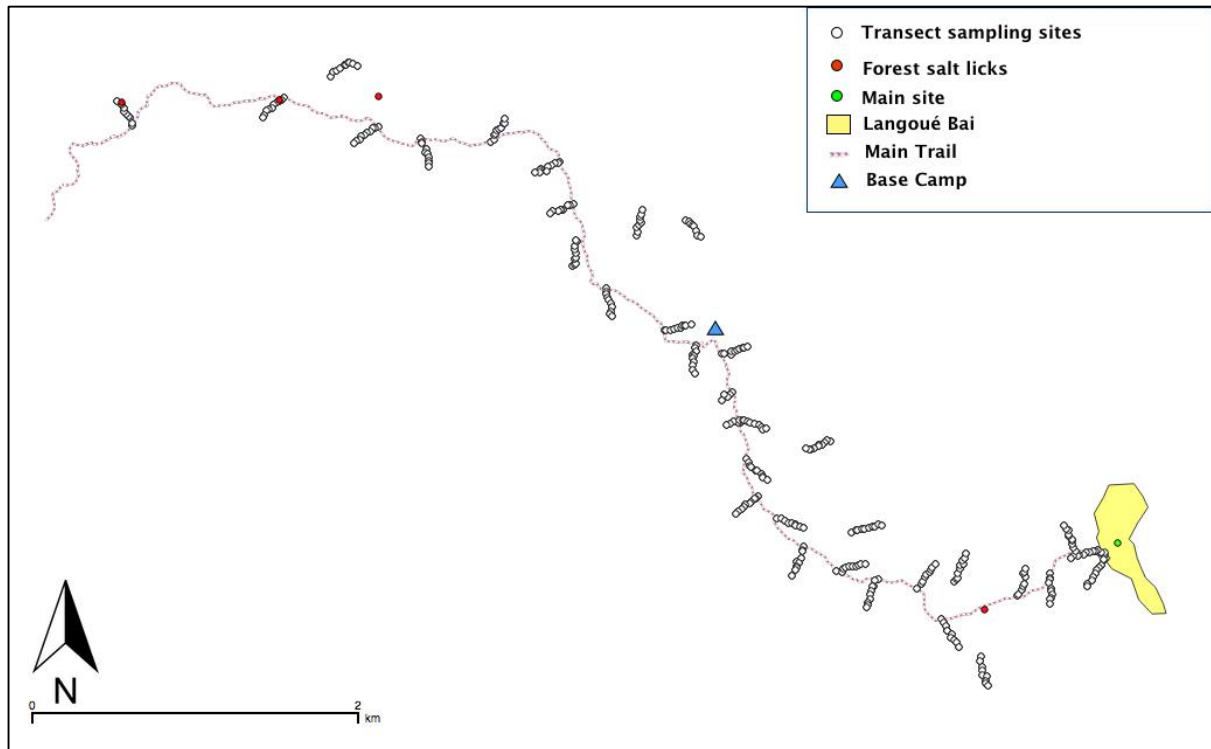
Figure.4. The location of sampling transects in relation to the main trail and the bai. Note that all the starting (0m) sampling sites were actually located on the main trail. The discrepancy between the location of the main trail and the starting points of a few transects visible on this figure is due to higher GPS accuracy (<5m) of the sampling site locations, than that of the trail location (~20-25m).

Twenty-nine 180 metre long transects were placed along the first 6.5km of the main trail (fig.4). Transects were oriented perpendicular to the trail, and soil and litter samples were collected every 20m, starting at 0m (i.e. on the trail itself). The first transect was placed at the start of the main trail, about 100m from the main site of elephant watering in the Langoué Bai (fig.4). The placement of the starting points of the remaining transects was determined according to idealised distances along the main trail mapped using the Quantum GIS version 1.8.0 geospatial software, and loaded into a GPS unit (Garmin GPSMAP 62s). Because the mineral concentration was expected to decrease in a logarithmic fashion with the distance from the bai, the intervals between transects were made smaller nearer to the bai. The starting point of each transect was navigated to using the GPS unit, and the remaining points on a transect were located using a compass bearing and 20m measuring tape. The side of the main trail on which the first transect was situated was chosen randomly, and thereafter, transects were located alternately on each side of the trail unless topographical obstacles were

encountered. The exact location along the main trail of some transects, or the side of the boulevard on which they were placed had to be modified on a few occasions, due the presence of obstacles such as rocks, swamps, or ant nests, and some transects had to be abandoned altogether. Some transects were also cut short for the same reasons, or due to the presence of dangerous animals (elephants or chimpanzees).

Within the studied length of the main trail, it was crossed by a number of other large and well used trails that could also be considered as local boulevards. To increase the spatial coverage of the study, six of these large trails were opportunistically followed, and an additional seven transects were placed there. To avoid bias in the location of the starting points of the transects off side trails, each side trail was followed for predetermined amount of time (15 or 30 minutes), and the starting point was then placed on the side trail exactly where I stopped. The side of trail on which the transect fell was chosen randomly.

A principal objective of this study was to test the effect of distance from a main trail on the distribution of minerals, and hence, the design involved collecting samples across a range of distances from main trails. However, in the field it was apparent that transects often crossed numerous other trails, some of which were wide and well compacted, suggesting frequent use of by elephants. More trails occur near the sites of interest to elephants, such as licks and large fruiting trees, suggesting that frequentation of an area by elephants is related to the density of elephant trails (Blake & Inkamba-nkulu, 2004). The density of trail network around different sites at Langoué was not uniform, and I therefore hypothesised that the distribution of nutrients dispersed by elephants in the forest might be related to the localised density of trails, rather than the distance from a main trail. In order to test this additional hypotheses, for each transect I recorded the location (at the crossing point) and width of each trail that crossed it. This information was computed into an index of trail density – the 'transect trail score' - which was the sum of widths of all trails crossed by a transect (including the main trail), divided by transect length.

2.3. Sample collection

At each sampling site, 6-15g of litter (i.e. surface organic matter) and 10-15g of mineral topsoil were collected from an area of around 10 cm^2. After clearing the site of litter and organic soil layer, mineral soil was collected with a spade from the top 5cm. At eight

randomly selected sampling sites, an additional two "field repeats" of litter and soil were collected from the same 10 cm^2 area, in order to assess within–site variability. Samples of litter and soil were air-dried in the field before transporting for lab analysis.

In addition to the hypothesised influences (i.e. distance from bai, and distance from elephant trail), nutrient concentrations could be expected to vary in relation to numerous biotic and abiotic conditions of the sampling sites. For example, the inclination and water content of a site may influence how quickly water soluble nutrients are lost from a site, while the density and type of vegetation could influence cycling and availability in both litter and soil. To attempt to account for, and to assess the relative importance of these influences, the following were recorded at each sampling site: *soil moisture* - measured at 12cm depth (in volumetric per cent) with a Campbell Scientific 620 /CS HydroSense TM unit; *inlicination* of the site – measured as the angle of slope (in degrees); and the *distance* in meters to the nearest tree with diameter at breast height of greater than 20cm.

Only one pre-existing sample from a hole in the main site in the bai, collected in February 2013, was available for this study. Further bai samples could not be collected at the time of fieldwork as elephant activity was too high.

During fieldwork, four small salines were encountered, where elephants had dug paddles or pits in the ground — about 1–2 meters deep and covering between 4 and 20 square meters — presumably to access the mineral–rich soil. The locations of these salines were recorded, and a sample of litter and soil was collected from one of them.

2.4. Laboratory Techniques

The laboratory techniques for elemental analysis of litter samples followed the dry ashing protocol from (Miller, 1998). Samples were dried at 65°C for 48h and then ground in a coffee grinder to pass through 40 size mesh. For each sample, 0.5 g ±0.05g of the ground material was placed in ceramic crucibles and combusted in a furnace, where the temperature was slowly ramped up to 500°C over the first two hours and then continued at 500°C for a further four hours. The ashes from each sample were then digested with 10ml 1M HCl and left in shaker at 250rpm over night. They were then filtered through Watmans No.42 papers and diluted to a volume of 500ml with deionised water. The resulting filtrate was analysed for Na, K, Mg and Ca content using an ion chromatographer (Dionex IC DX500). To asses the proportion of variation in mineral concentrations attributable to natural variation at single site

and to the error introduced by laboratory methods (lab error), additional repeats were analysed for a variance components analysis on a subset of litter samples: 3 field repeats from 8 different sites were analysed; for 14 of the field repeats three lab repeats were analysed, of which 30 were read twice by the chromatographer. In total, there were 60 observations of duplicate chromatograph readings, nested within 42 lab repeats, nested within 24 field repeats, nested within 8 different sites.

Soil samples were analysed for water–soluble cation content. The samples were dried at 35°C for two weeks, then lightly crushed to pass through a 2 mm mesh. For each sample, one gram of soil ±0.02 g was dissolved in 50 ml deionised water, shaken at 250 rpm for an hour, and left in an ultrasonic bath for an hour. The solution was then passed through Whatman grade 42 filter paper and diluted to 100 ml with deionised water. The resulting filtrate was analysed for Na, K, Mg and Ca content using an ion chromatographer (Dionex IC DX500).

2.5. Statistical analysis

In ecological science, it is often desirable to assess a number of explanatory variables to determine which, if any, are useful predictors of variation in a response variable. The traditional approach has generally involved step-wise comparison and simplification of nested models, until a model is identified that contains only the predictors that are deemed to explain significant amount of variation in the response variable. However, this has drawn criticism due to its sensitivity to the model simplification algorithm used, and for problems associated with multiple hypothesis testing (Calcagno & de Mazancourt, 2010). An alternative approach increasingly gaining popularity is based on Information Criteria (IC), such as the Akaike Information Criterion (AIC). Information criteria measure relative model performance using the deviance, and penalise for the number of estimated parameters. Models containing all combinations of the considered predictors can be ranked by their IC scores and the best approximating model can be identified. In cases when differences in IC score between multiple models are small and no single model appears to be clearly the 'best' one, model averaging may be employed to account for uncertainty in model selection. Estimates of each parameter are averaged across all possible models, but the influence of each estimate is weighted by the performance of the model to provide robust parameter estimates and confidence intervals (Grueber, Nakagawa, Laws, & Jamieson, 2011).

This study employed an IC-based model averaging approach. All statistical analysis was performed using R version 3.0.0 (R Development Core Team, 2013). The concentrations of all elements displayed a left skew, and so a natural log–transformation was applied prior to analysis. Data were analysed using generalised linear mixed effects models, implemented with the *lmer* function in the *lme4* package (Bates, Maechler, & Bolker, 2013). It is expected that there would be autocorrelation of samples within transects, and within trails, so transect identity and trail identity (main trail or one of the six crossing boulevards) were fitted as random effects in all models. For each analysed element, a global model was fitted relating the log-transformed mineral concentration with the following as fixed effects: *distance from bai* (m); *distance from closest tree* (m); *cline* (degrees), *soil moisture* (%); and either *distance from main trail* (m) or *transect trail score*. As the *distance from main trail and transect trail score* both attempt to measure the effect of trails on element concentrations, two versions of the global model were considered, each including only one of these two predictors. To account for the possibility of non-linear relationships with distances, quadratic transformations of the three distance variables were included in global models.

For each global model, the predictor variables were standardised following the recommendations of Grueber et al (2011), and a set of models with all combinations of the terms in the global model was generated. Relative performance of competing models was measured using the corrected Akaike Information Creterion (AICc) (Hurvich & Tsai, 1989). Parameter estimates for predictor variables were averaged across all models, weighted by model performance. Predictors for which the parameter estimate 95% confidence intervals did not include zero were inferred to have a significant effect on the response variable and were included in the approximating model. If a quadratic term in the model showed significant effect, its non-quadratic form was also included in the approximating model. The results were then visualised using the *plotMER.fnc* function in the *languageR* package (Baayen, 2011). Overall model performance was assessed using marginal R^2 for generalised mixed effect models ($R^2_{GLLM(m)}$), which is the proportion of variance explained by fixed effects, and conditional R^2 ($R^2_{GLLM(c)}$), which can be interpreted as the variance explained by the entire model (Nakagawa & Schielzeth, 2013). Models were assessed for normality of errors and heteroscedacity using q-q plots, and plots of standardised residuals against fitted values (Crawley, 2007, p.281, 340)

To assess the proportion of variance attributable to mineral concentration heterogeneity at same site, and to measurement error (i.e. variation introduced by the laboratory processing or machine use), mineral concentration was analysed using a model with no fixed effects, and with random effects for *Site* (n=8), *field repeat* (n=24) nested within site, and *lab repeat* (n=42) nested within field repeat. Variance in chromatographer readings for the same lab repeat was captured by the residual (n=60). The proportion of variance explained by a particular effect was obtained by dividing the variance estimate for that random effect by the sum of the random effect variances.

2.6. Lateral Diffusion Model

The Lateral Diffusion Model from (Wolf, Doughty, & Malhi, 2013) was used to generate possible scenarios of nutrient diffusion by herbivores at Langoué. The actual values for most parameters were unknown, but plausible estimates from other sources were used. Thus, the rate of loss was fixed at 0.001, based on the loss rate calculated for Phosphorous from the mechanistic model of Buendia et al. (2010). The nutrient in the bai in kg/ha was calculated for Ca (as the most abundant mineral in the study set) and Na (as the least abundant mineral) in the following way: mean concentrations for Ca and Na from this study were multiplied by the ratio of bai/forest mineral concentrations in soil of the bai in the Hakou aera in Dzanga NP. This was 5.6 and 8.5 for Ca and Na, respectively. These values was converted into kg/ha using the estimate of average litter–fall for West Africa, which is 7000 kg/ha (John, 1973). The diffusivity coefficients for different species were calculated as a function of size, using allometric equations for consumption rate, daily displacement, abundance, range size, and gut passage time (for exact method see Wolf et al., 2013 SOM, pg.9). The diffusivity of the whole community was based on those species estimates from Serengetti, which was readily availbale. Because the river that runs through the bai (and presumably exposes mineral deposits) is only a small tributary of the Langoué River, it is likely to have been dry, or to have had a different course during the recent arid periods in Africa. Within the last 20,000 years, one major arid phase, during the last major global and regional period, lasted from 20,000 to 10,000 B.P., and another short and intense arid period occurred between 2,800 to 2,000 B.P. The bai was more likely to form during wet periods, so either sometime between 10,000 and 2,800 B.P. or within the last 2,000 years. Therefore, a timescale of 10,000 years that encompasses both of the wet periods was chosen for the model.

3. Results

Time constraints imposed a limit on the number of samples that could be analysed. For most transects, only every second litter sample (from sites at 0m ,40m, 80m, 120m, and 160m from the trail), and only two soil samples (from sites at 0m and 80m), were analysed. In total, I obtained results for litter samples from 194 sites, and soil samples from 64 sites. The mean concentrations and 95% confidence intervals for litter were 0.04±0.02 mg/g for Na, 1.0±0.5 mg/g for K, 0.8±0.4 mg/g for Mg, and 4.4±2.3 mg/g for Calcium. Individual measurements ranged from 0.01–0.15 mg/g for Na, 0.2–3.3 mg/g for K, 0.1–2.3 mg/g for Mg, and 0.8–13.7 for Ca. The water-soluble concentrations from soil were, as expected, generally lower than the litter concentrations, with means of 20.6±6.6 mg/kg for Na, 30.9±14.6 mg/kg for k, 9.3±2.6 mg/kg for Mg, and 58.3 mg/kg for Ca. The ranges included 11.9–41.1 mg/kg for Na, 11.3–82.1 for K, 4.75–18.32 for Mg, and 36.1–111.7 for Ca.

The results of the variance components analysis for the contribution of different sources of error to variation in mineral concentrations are presented in table1. In total, there were 60 observations of duplicate chromatograph readings, nested within 42 lab repeats, nested within 24 field repeats, nested within 8 different sites. The variance between chromatographer readings for the same solution was always less than 0.01% of the total variance, and so these are not presented. The majority of the variance in Ca and Mg concentrations occurred between sites (87% and 69%, respectively), supporting the later analysis where a single observation per site was used to investigate patterns in the concentrations of these elements. However, in the subset of the samples used for this analysis, laboratory error accounted for 41% of the variance in Sodium concentrations (0.01 mg/g in absolute terms), whilst whitin-site variation accounted for 63% (0.43 mg/g in absolute terms) of variance in Potassium. For this reason, the results of subsequent analysis for these elements should be interpreted with caution.

Table 1. Proportion of Variation in Litter Nutrient Concentration due to Different Sources of Error

Component	Relative proportion of variation in concentrations				Variation in concentrations in absolute terms (mg/g)			
	Ca	Na	Mg	K	Ca	Na	Mg	K
Total	1.00	1.00	1.00	1.00	3.36	0.02	0.49	0.67
Between-Site	0.87	0.23	0.69	0.34	2.91	0.00	0.34	0.23
Within-Site	0.13	0.35	0.30	0.63	0.42	0.01	0.15	0.43
Lab Error	0.01	0.41	0.01	0.02	0.02	0.01	0.00	0.02

No clear patterns in relation to distance from the Main Trail or distance from the bai were apparent from maps of spatial distribution of mineral concentrations (fig.5), although there appear to be clusters of higher values for all minerals around the mid-distance and towards the end of the Main Trail. Those near the end of the Trail seem to be all in the vicinity of one of the salines (marked in red on fig.5). This may indicate that higher values are associated with the presence of salines, and there may be additional salines that have not been encountrered during the study. Scatterplots of the mineral concentrations and the various explanatory variables are presented in figure 6.

The approximating models for mineral concentrations in litter contained various predictors (see table 2). Sodium concentration showed a relationship with the squared distance from the bai, with concentrations increasing slightly to a peak at around the middle of the Main Trail, and then dropping off with increasing distance (fig.7). The humped shape of this relationship appears driven by a small number of relatively high concentration points near the middle of the trail. However, when these points were removed from the dataset to assess their leverage, the shape of the relationship changed only minimally. Another significant effect was the positive relationship of Na concentrations with the squared distance from the tree which caused decrease in Na concentration with increased distance from closest tree. Overall the approximating model explained 43% of variation in Na concentrations, of which 16% was due to fixed effects. Nonetheless, this result should be approached with caution because of the large effect of the lab-error on variance of sodium concentrations (table.1).

Potassium was significantly related only with soil moisture, which explained 7% of the variation, with 31% of the variation explained by the whole model. Magnesium concentration was mildly positively related to distance from the bai, and negatively related to soil moisture. Fixed effects explained around 12% of the variation, whilst

the overall fit of the model to the data was 42%. Calcium showed similar pattern to Na in that it was related to distance from the bai, and negatively related to distance from nearest tree, although quadratic terms were not significant. Fixed effects explained 8% of variation in response, and overall the model explained 33%. The modelled relationships between the mineral concentrations and their significant factors are presented in figure 6.

Table.2. Summary of approximating models for element concentrations in litter and soil

element	significant effects	Sign	$R^2_{GLLM(m)}$	$R^2_{GLLM©}$
	Aprroximating model summary			
Na, litter			0.16	0.43
	Distance from the bai*	NA		
	Distance from the bai squared	(-ve)		
	Distance from nearest tree*	NA		
	Distance from nearest tree squared	(-ve)		
K,litter			0.07	0.31
	Soil moisture	(-ve)		
Mg, litter			0.12	0.42
	Distance from the bai	(+ve)		
	Soil moisture	(-ve)		
Ca, litter			0.08	0.33
	Distance from the bai	(+ve)		
	Distance from nearest tree	(-ve)		
Na, Soil	none	NA	-	-
K, Soil	lack of model convergence	NA	-	-
Mg, Soil**			0.20	0.52
	Distance from Main Trail	(-ve)		
Mg, Soil***			0.20	0.40
	Soil Moisture	(+ve)		
Ca, Soil	Distance from the bai	(+ve)	0.07	0.43

*Effect *included in the model because its quadratic form was significant*
***The significant terms in the model of magnesium in soil differed depending on whether Distance from Main Trail, or the Transect Trail Score were included in the global model. See explanation in text*

Litter Na (mg/g)

○ 0.0127 - 0.0411
○ 0.0411 - 0.0694
○ 0.0694 - 0.0978
● 0.0978 - 0.1262
● 0.1262 - 0.1545

N

0 ▬▬▬▬ 1 km
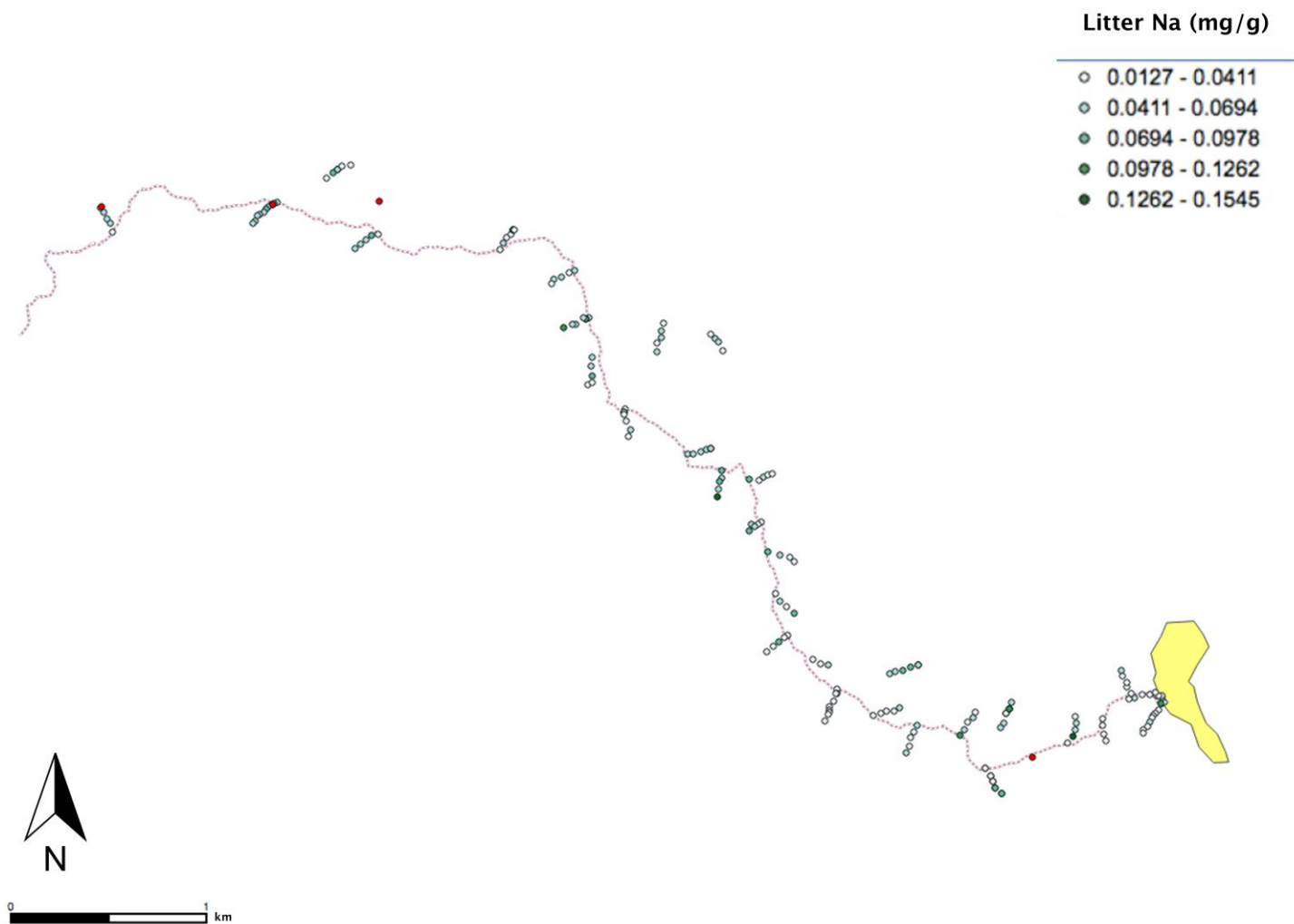
Figure .5. Maps of nutrient concentrations along the Main Trail (continues on following pages)

Litter K (mg/g)

○ 0.2222 - 0.8443
○ 0.8443 - 1.4664
○ 1.4664 - 2.0884
● 2.0884 - 2.7105
● 2.7105 - 3.3326

N

Figure 5. continued

Litter Mg (mg/g)

- ○ 0.1277 - 0.5705
- ○ 0.5705 - 1.0132
- ○ 1.0132 - 1.4559
- ● 1.4559 - 1.8986
- ● 1.8986 - 2.3413

N

Figure 5. continued

Litter Ca (mg/g)

- ○ 0.7669 - 3.3507
- ○ 3.3507 - 5.9344
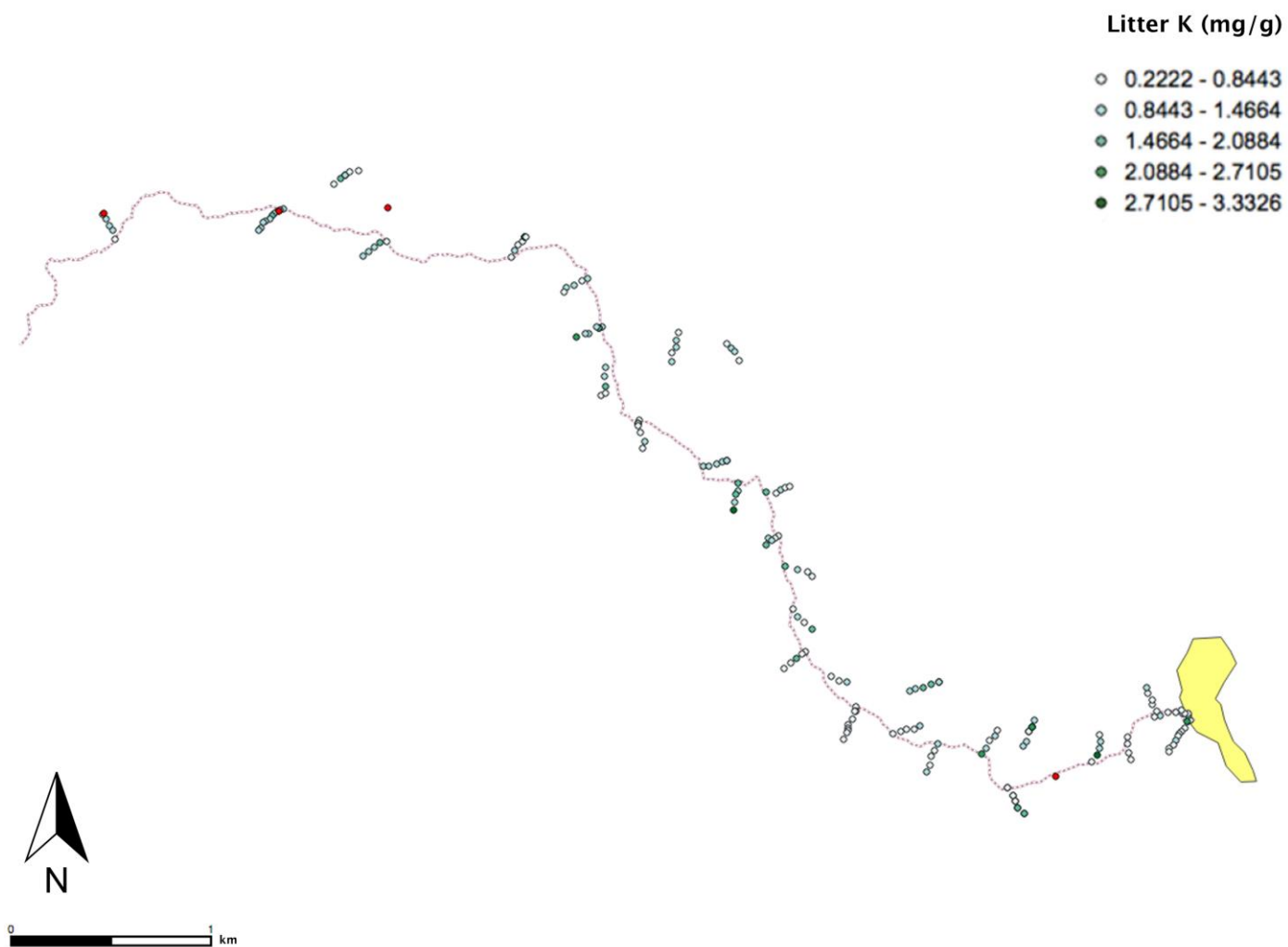- ○ 5.9344 - 8.5182
- ● 8.5182 - 11.1019
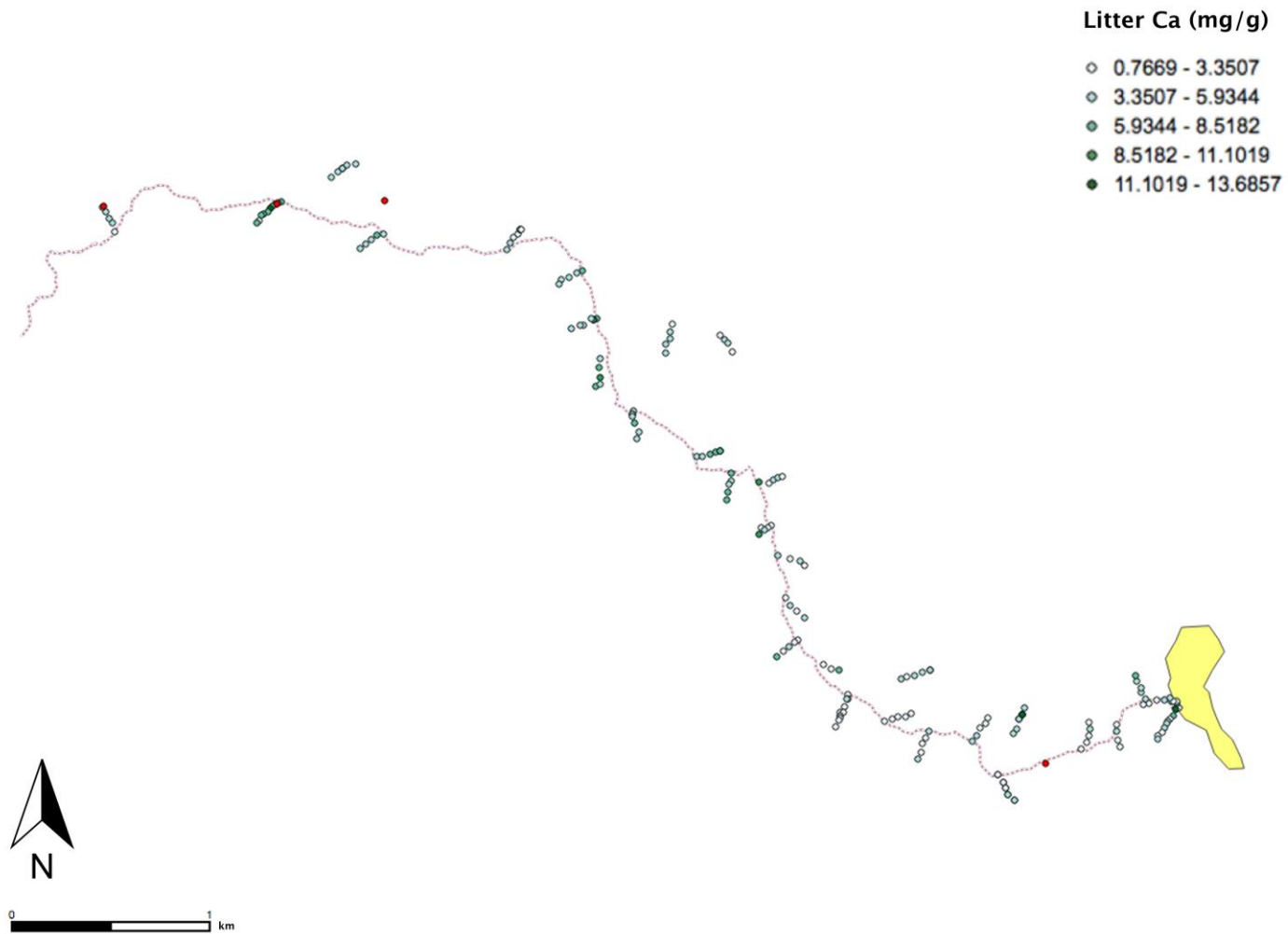- ● 11.1019 - 13.6857
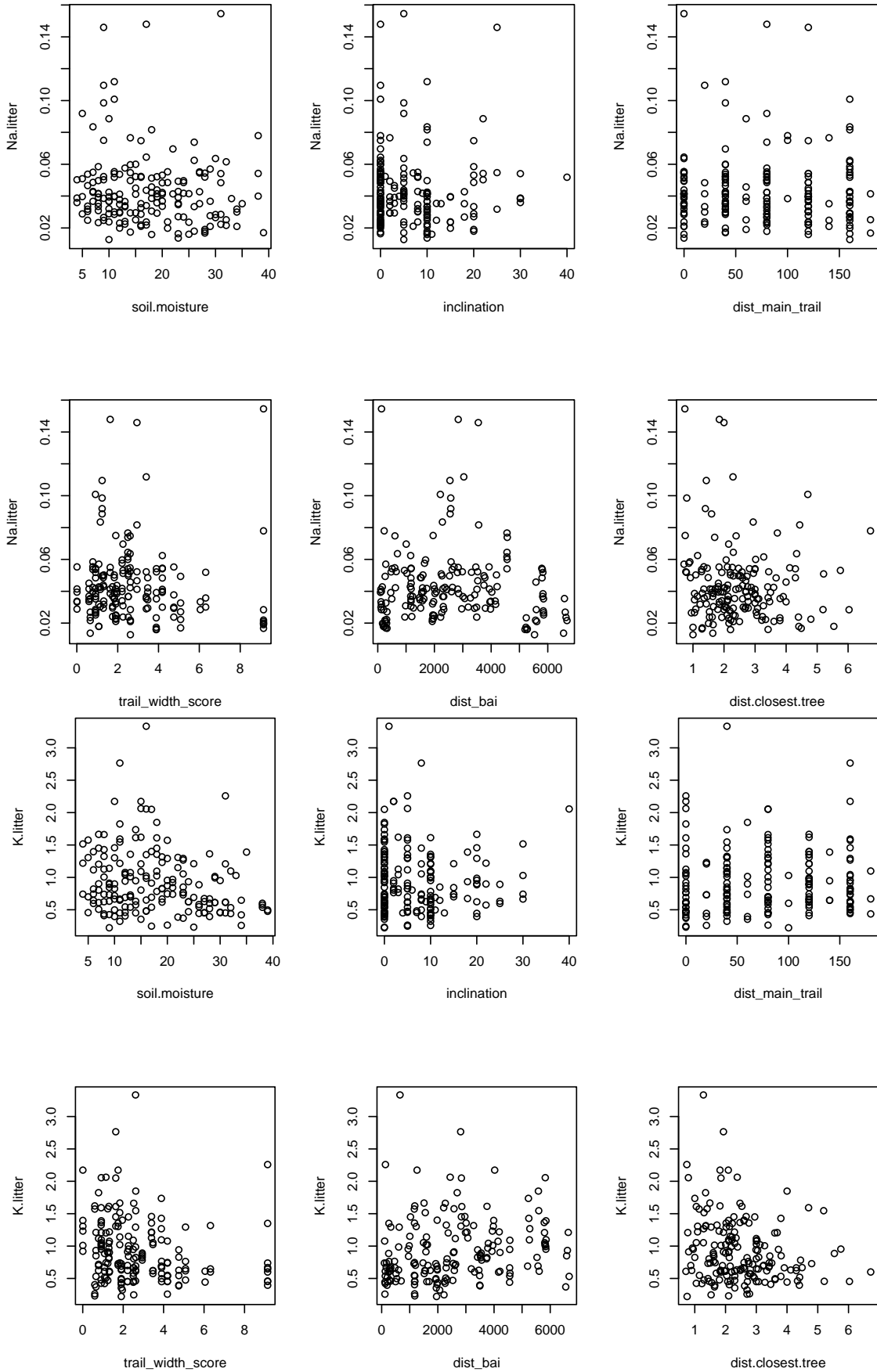
N

0 ▬▬▬▬▬ 1 km

Figure 5. continued

Figure 6. Scatterplots of mineral concentrations in litter and water-soluble soil vs. explanatory variables. Mineral concentrations are in mg/g for litter, in mg/kg for soil. soil.moisture = volumetric % soil moisture at 12cm depth. inclination = terrain inclination in degrees (integer numbers only). dist_main_trail = Distance from the Main Trail in meters. Trail_width_score = Transect trail score. dist_bai = Distance from the bai in meters. dist_closest_tree = distance in meters to closest tree trunk of DBH >20cm. Figure is continued on following pages.
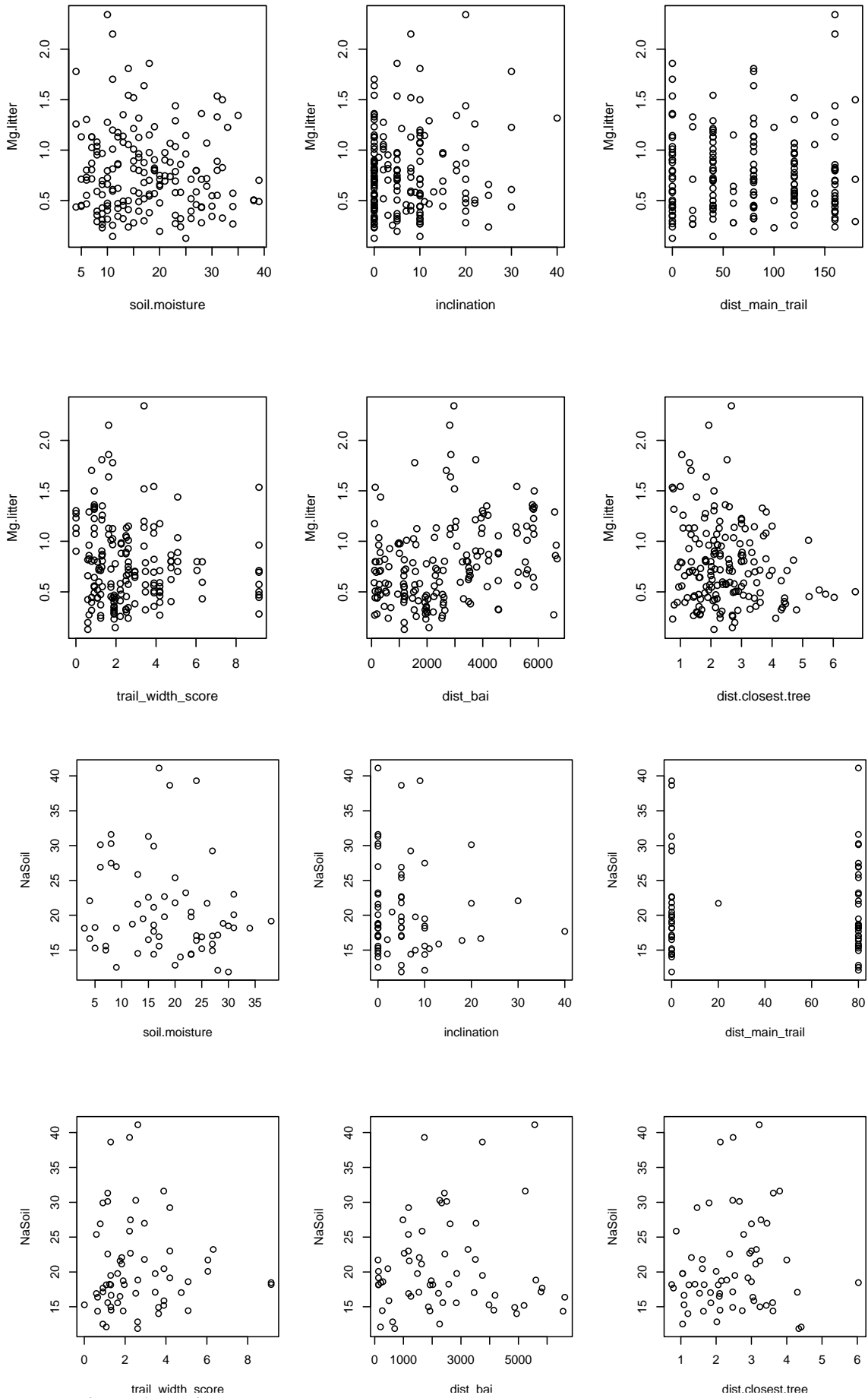
Figure 6. continued.

Figure 6. continued.
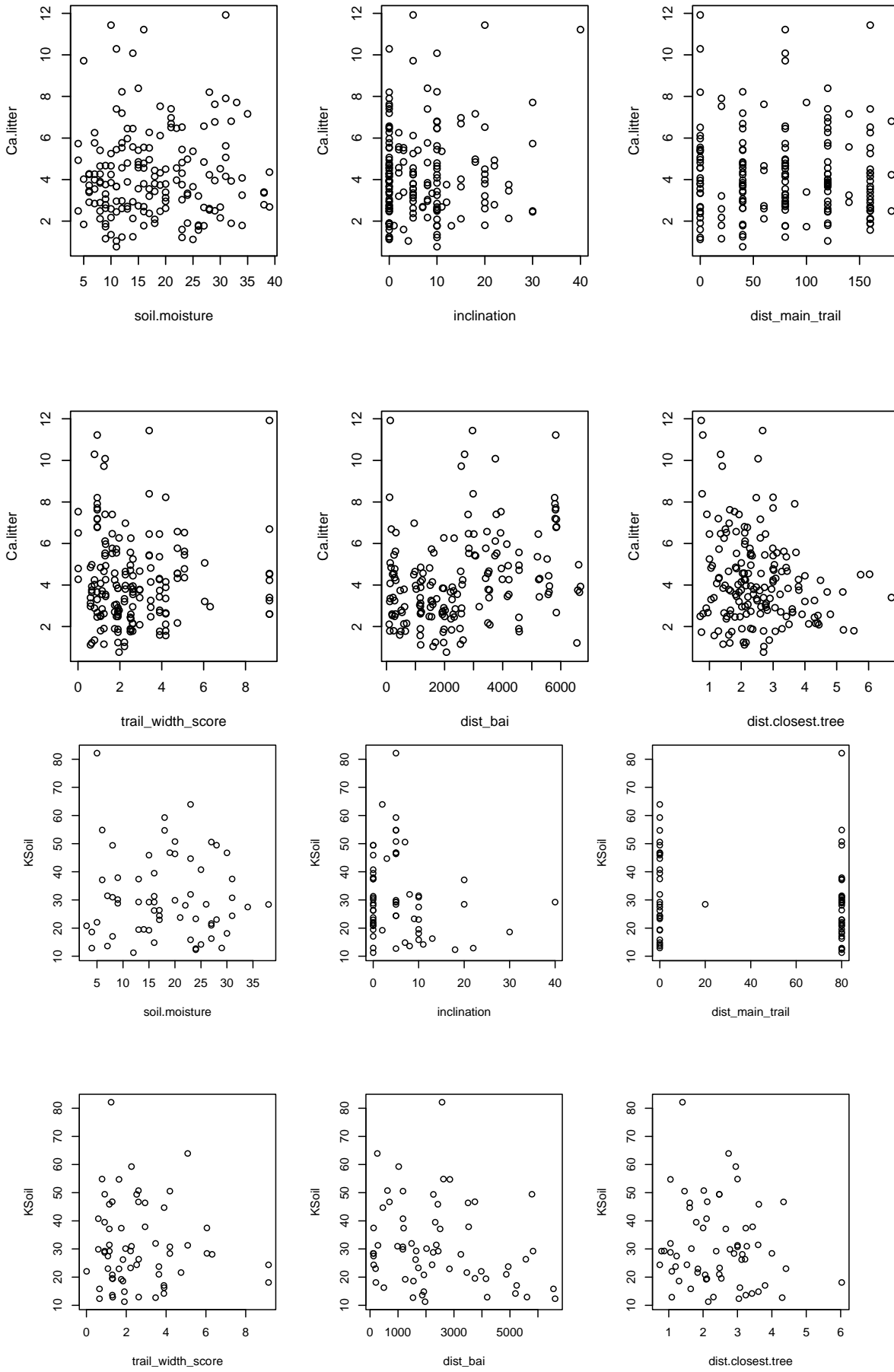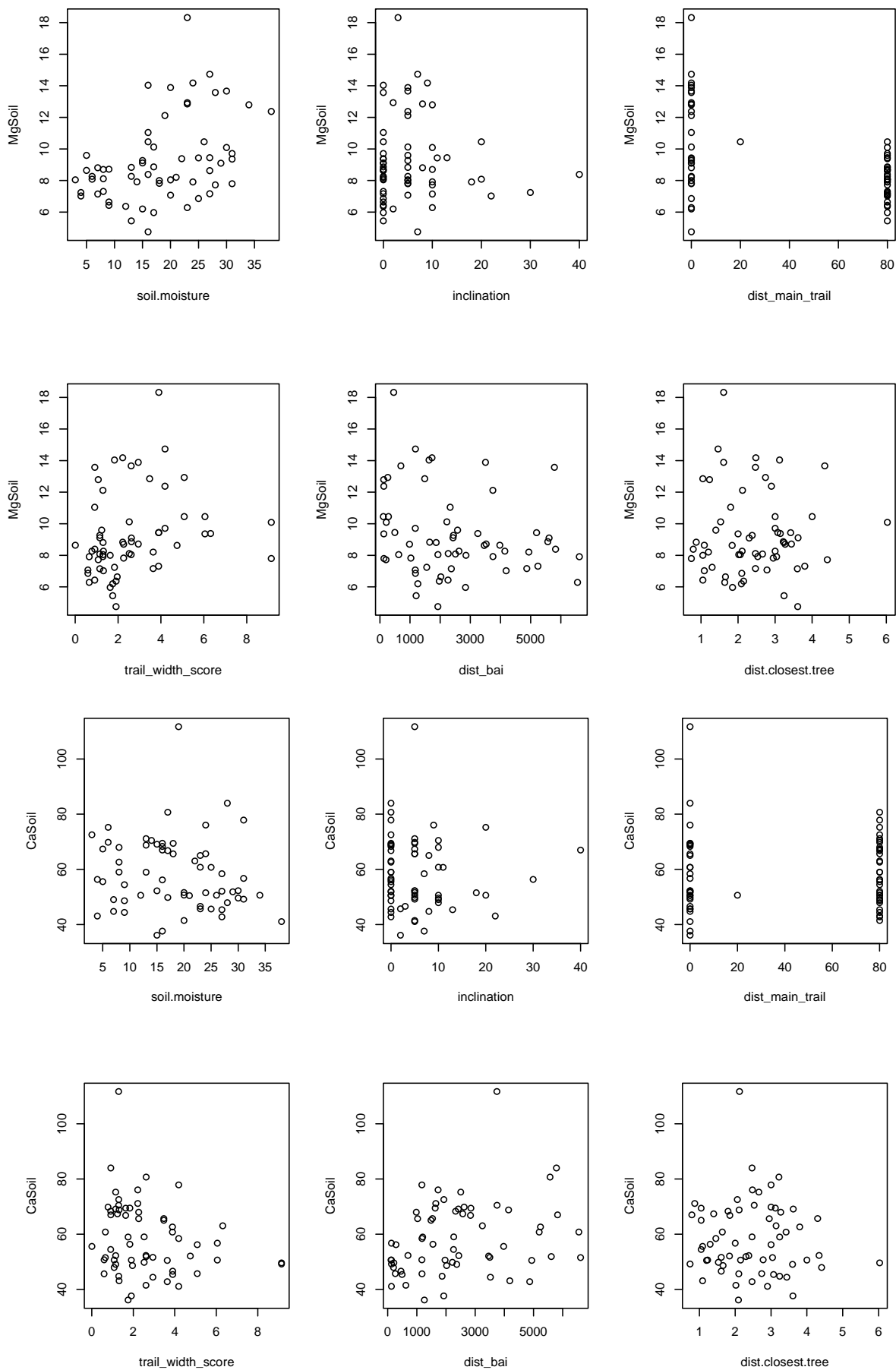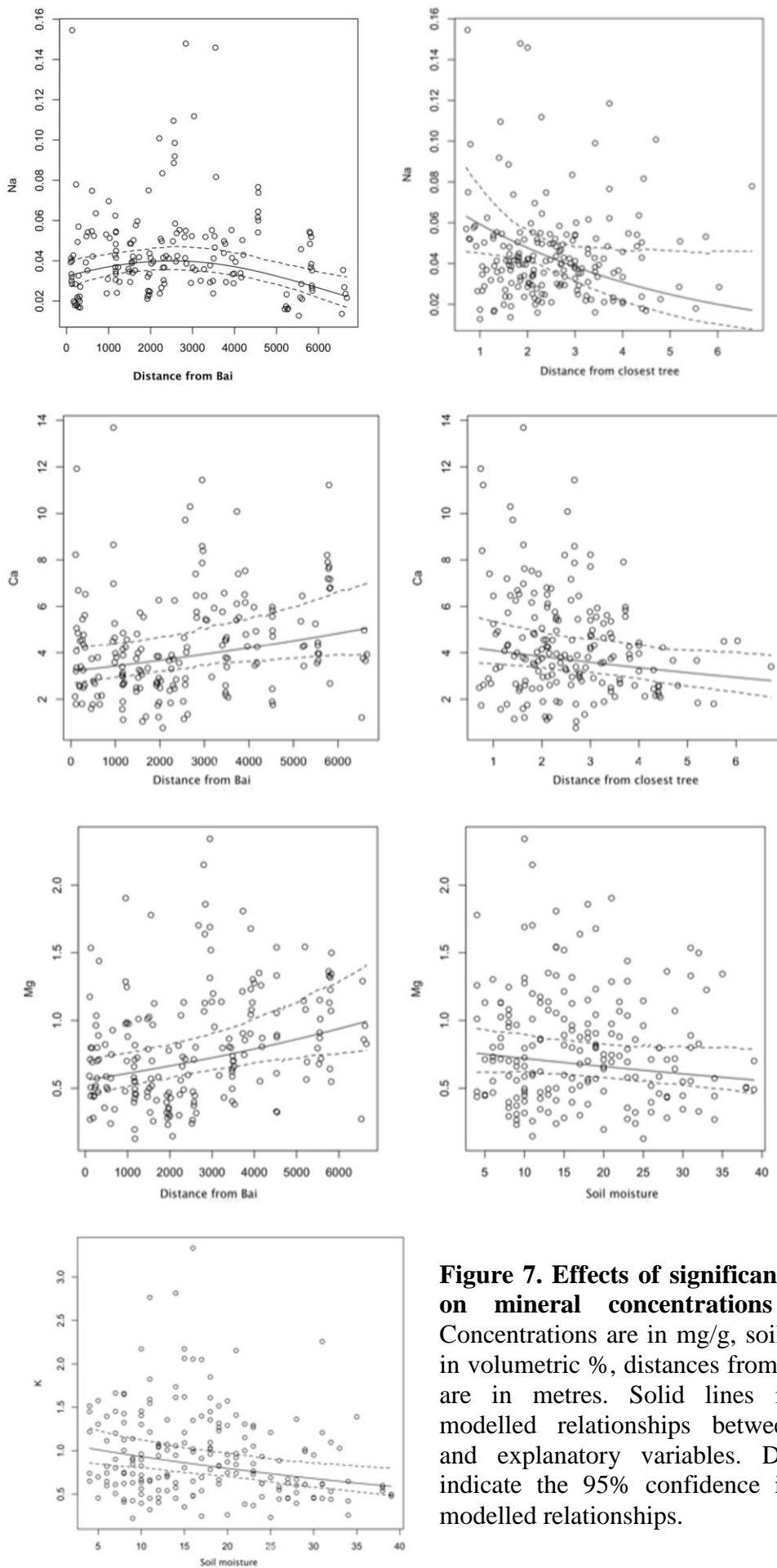
Figure 6. continued.

Figure 7. Effects of significant predictors on mineral concentrations in litter. Concentrations are in mg/g, soil moisture is in volumetric %, distances from bai and tree are in metres. Solid lines indicate the modelled relationships between minerals and explanatory variables. Dashed lines indicate the 95% confidence intervals for modelled relationships.

In the analysis of water-soluble element concentrations in soil, no significant effect was identified for sodium, either because none was included among the tested variable set, or possibly, due to the low power of the model. For potassium, the models failed to converge, even after the size of the model was reduced to contain just the random effects and a single fixed effect. This is probably a result of over-parameterisation relative to the number of samples and total variation. For magnesium there were no apparent problems with model convergence, but the terms included in the approximating model differed depending on whether the global model included the "distance from the Main Trail" or the "Transect Trail Score". In the former case, the distance from the Main trail was the only significant factor, explaining 20% out of 52% of variation explained by the model. When the Transect Trail Score was included, the only significant factor was moisture, which accounted for 21% out of the 40% of variation explained by the model. Thus, the averaged model with distance from Main Trail seems to have a better fit. The models of calcium concentration converged properly and both identified a positive relationship with distance from the bai as the only significant effect (fig.8). This result is consistent with that for calcium in litter, whose concentration also increased slightly away from the bai.

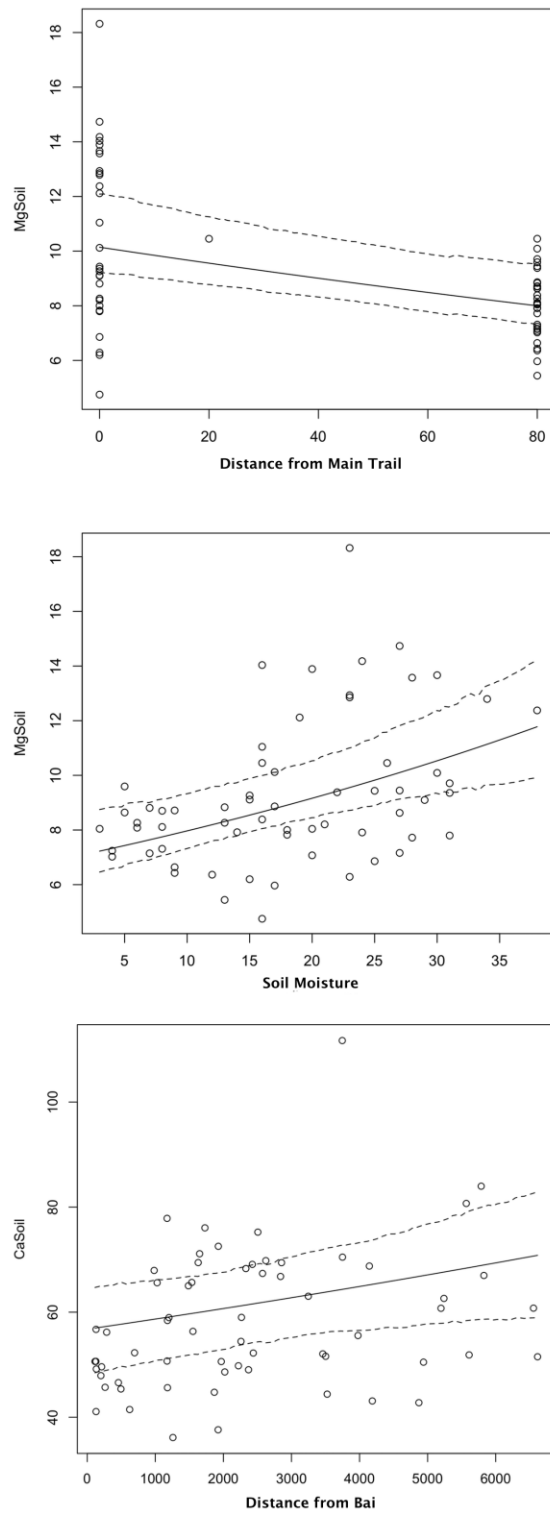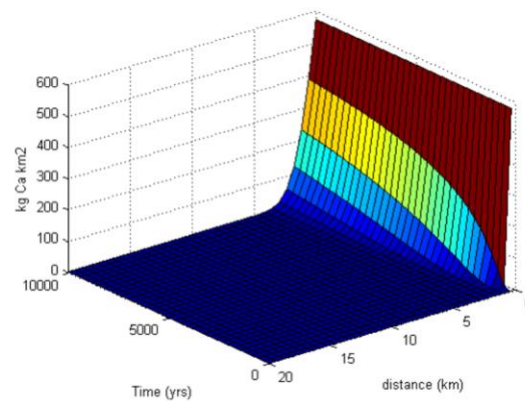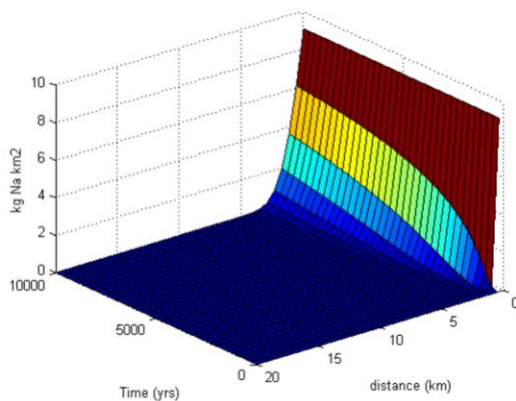**Figure 8. Effects of significant predictors on mineral concentrations in water-soluble soil.**
Distances from the Main Trail and from the Bai are in metres, soil moisture is in volumetric % at 12cm depth. Dashed lines indicate 95% confidence intervals for parameter estimates. Note that the significance of moisture effect on Mg concentration was dependent on terms included in global model. See text for further explaination.

The results of the Lateral Diffusion Model for Langoué are presented in figure 9. Assuming the age of the bai to be around 10,000 years, for a distance of about 7 km, we observe a change in Ca of ca. 20–40 kg/ha, depending on whether we consider diffusion by elephants only, or by the whole herbivore community. Under the assumption of 7000 kg/ha litter production, this translates to a difference in concentration of about 3 to 6 mg per gram of edible biomass. For Na, where the expected budget is much smaller (only around 9 kg/ha in the bai above the background forest rates), when we consider diffusion by all herbivores this difference may be as low 0.1 kg/ha , or 0.01 mg/g of plant biomass. Such difference should be detectable by the methods used in this study, provided other sources of variation are controlled for.

Because the values for many parameters in the model, including mineral concentrations in the bai, mineral loss rate, and herbivore biomass are "best guesses" based on other studies, the exact numbers are probably misleading. However, they should be indicative of the order of magnitude of the difference that could be expected if the bai is indeed an important source of minerals in this landscape. If the change of mineral concentration over 7 km due to lateral diffusion by animals is at least 1kg/ha, or ~0.14 mg/g, it should be reliably detectable even considering the effect of lab error (see table 1). The change (in absolute terms) is likely to be the lowest for sodium, owing to its low levels in the system.

Figure 9. Simulations of nutrient concentration gradients in edible plant matter created through diffusion by the vertebrate herbivore community at Langoué. **Φ = diffusivity coefficient.**

5.Discussion

Observed concentrations

A comparison with other literature indicates that the concentrations of litter observed in this study are somewhat low, but within the expected range for tropical humid forests (table.3). In particular, the means, ranges, and ratios of the different elements are very similar to those obtained for litter in rain forests in Sarawak, Malaysian Borneo (Anderson, Proctor, & Vallack, 1983).

Similarly, the results for water soluble soil cation concentrations fall within the expected ranges, and close to the median values obtained by Sharpley & Kamprath (1988) for a large sample representative of many major soil types around the world (table.4). Unfortunately, exchangeable cations (a total measure of plant–available nutrients) values could not have been obtained for this study, due to limitations in equipment. The water-soluble cation values measur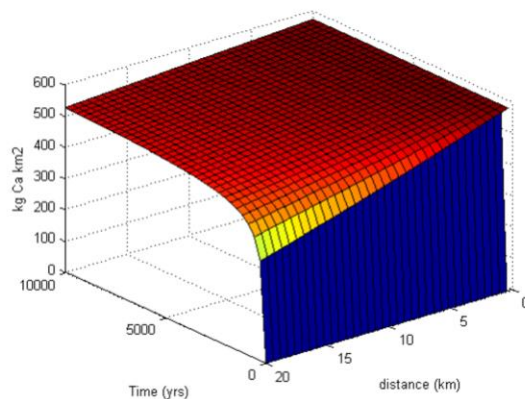ed here can only be compared between samples coming from the same soil type, because the proportion of exchangeable cations that is water soluble varies greatly with soil properties such as texture and cation specific exchange complex saturation rates (Sharpley & Kamprath, 1988), the establishment of which was beyond the scope of this study. This precludes comparisons between the forest and bai soils, as well as comparisons with published data.

Relationships with distance from bai

Multi-model inference across sets of mixed effects models revealed various significant relationships between the concentrations of minerals in litter and the considered predictor variables. For sodium, a significant relationship with distance from bai was identified, with concentrations initially increasing slightly and then decreasing with increasing distance from the bai. This is at least partially congruent with the primary hypothesis that salts decrease in concentration with increasing distance from the bai. Furthermore, the distribution of concentrations is compatible with animal-mediated dispersal (fig.9., medium and bottom panels), indicating a

gradual decline with increasing distance from the bai, rather than a discrete step-change decrease (fig.9. top panel).

Table. 3. Mean Litter Nutrients for Tropical Forests with above 1,500mm Annual Precipitation

Citation	Place	Forest type	Precipitation (mm)	Litter Nutrient(mg/g)			
				K	Ca	Mg	Na
Veneklaas(1991)	Columbia	Lower Montane	1,500	3.5	-	-	-
Brasell *et al.* (1980)	Australia	Rain forest	1,500	6.4	21.1	3.2	0.40
Maheut & Dommeregues (1960)	Senegal	*Tectona* Plantation	1,590	7.0	17.5	3.5	-
Enright(1979)*	New Guinea	Lowland rain forest	1,600	0.3	2.1	0.1	0.10
Nye & Greenland (1960)	Ghana	High forest	1,630	6.5	19.6	4.3	-
Laudelot & Meyer (1954)	Congo	Plateau forest	1,700	3.9	8.5	4.3	-
Berhard-Reversat (1972)	Ivory Coast	Rain forest (Yapo I)	1,735	2.8	13.2	2.9	-
		Rain forest (Yapo II)	1,735	4.9	13.6	3.2	-
Present Study*	**Gabon**	Rain forest	1,750	1.0 ± (0.5)	4.4 ± (2.3)	0.8 ± (0.4)	0.04 ± (0.02)
				[0.2-3.3]	[0.8-13.7]	[0.1-2.3]	[0.01-0.15]
Cornforth (1970)	Trinidad	*Mom excelsa* forest	1,800	1.6	9.1	2.2	-
Swamy & Proctor (1994)	India	Moist deciduous	1,900	7.2	21.5	5.5	0.50
Klinge & Rodriguez (1968)	Brazil	Tierra Firme	1,900	2.0	2.5	2	0.70
Ewel(1976)	Guatemala	Secondary forest	2,000	2.4	21.2	3.5	-
		Mature forest	2,000	2.2	9.8	7.1	-
Lim (1978)*	Malaysia	Dipterocarp rain forest	2,000	3.7	7	2.2	-
Golley *et al.* (1975)	Panama		2,000	5.6	28.9	2.5	0.20
Bernhard (1970)	Ivory Coast	Rain forest (plateau)	2,095	2.5	9.4	3.8	-
		Rain forest (valley)	2,095	7.0	11.6	3.7	-
Veneklaas(1991)	Columbia	Lower Montane	2,115	8.9	-	-	-
Golley et al. (1975)	Panama	Premontance wet forest	2,500	5.0	14.7	2.3	0.30
Herbohn & Congdon (1998)	Australia	Upland rain forest	2,630	4.3	9.7	2.8	-
Fölster & de las Solas (1976)	Columbia	Humid tropical forest	3,000	2.3	10.8	1.6	-
Cuevas & Medina (1986)	Venezuela	Tierra Firme	3,565	2.4	1.7	0.7	-
		Tall Caatinga	3,565	2.1	7.7	3.1	-
		Bana	3,900	4.7	7.4	2.5	-
Swamy & Proctor (1994)	India	Lowland rain forest	4,000	5.8	20.3	5.8	0.60
Edwards (1982)	New Guinea	Lower Montane	4,200	3.9	12.5	2.7	-
Jordan *et al.* (1982)	Puerto Rico	Lower Montane	4,300	0.4	8.3	2.1	-
Gessel *et al.* (1980)*	Costa Rica	Rain forest	4,300	4.1	17.9	-	-
Wood *et al.* (2006)	Costa Rica	Rain forest (inceptisol)	4,300	3.3	8	2	0.50
		Rain forest (ultisol plateau)	4,300	2.0	8.3	2.3	0.60
		Rain forest (ultisol slope)	5,000	2.4	7.1	2	0.60
Rai & Proctor (1986)	India	Rain forest	5,000	2.7	11.2	4.5	-
		Rain forest	5,000	1.9	11.4	8.7	-
		Rain forest	5,000	4.1	11.5	9	-
		Rain forest	5,000	1.5	7.6	3.2	-
Proctor (1984)	Malaysia	Alluvial forest	5,000	2.6	24.4	2	-
		Keranga	5,000	2.3	8.8	1.6	-
		Dipterocarp rain forest	5,000	4.5	1.5	1.1	-
		Calcareous	5,000	1.6	31.8	3.3	-
Anderson *et al.* (1983)	Malaysia	Alluvial forest	5,090	3.9	20.5	2.1	0.03
		Dipterocarp rain forest	5,110	3.7	3.7	1.1	0.03
		Heath forest	5,700	1.3	5.5	1.2	0.03
		Forest over limestone	5,700	0.9	35.0	2.7	0.11
Swamy & Proctor (1994)	India	Lowland rain forest	6,400	6.6	13.8	3.9	0.90
		Lower Montane	6,400	6.5	16.3	5.8	0.80
Mean				3.7	12.9	3.2	0.40

*Indicates studies where leaf litter was collected on the ground

± ( ) = ±(Standard Deviation), for present study

[ ] = minimum ro maximum range, for present study

Information in this table was compiled from primary data in Anderson *et al.* (1983) and data reviewed in similar table by Wood *et al.*(2006)

Table.4 Water-Soluble Soil Nutrient Concentrations

		Water Soluble Soil Nutrient concentrations (mg/kg)			
		Na	K	Mg	Ca
Present study	mean	20.6	30.9	9.3	58.3
	SD	6.6	14.6	2.6	13.2
	range	11.9-41.1	11.3-82.1	4.75-18.32	36.1-111.7
	Bai sample**	24.9	25.4	7.9	132.2
	Salt lick sample	41.3	16.2	9.4	142.0
Sharpley & Kamprath (1988)	mean	69.0	81.0	22.0	94.0
	median	9.0	39.0	9.0	30.0
	range	1.0-3544	1.0-911	1.0-605	1.0-6528
	ratio range*	1.3-24.1	1.2-10.4	6.3-105.5	2.5-170.1

*Ratio represents the exchangable to water soluble content of each cation
**Note that due to lack of reliable relationshio betweeen exchangeable and water soluble cation content, the values for soils from the forest and the bai are not directly comparble

Significant relationships with distance from the bai were also identified for Ca and Mg in the litter, and for Ca in the soil, but in these cases, concentrations increased with increasing distance from the bai. Such a pattern is clearly incongruent with the primary hypothesis that salts decrease in concentration with increasing distance from the bai, and hint at the possibility that the bai does not represent a significant source of K, Mg, and Ca in the forest. Alternatively, if there is a gradient of nutrient concentrations in plant tissues, it may be too flat to be captured on the spatial scale of the present study. Based on the Lateral Diffusion Model, this could be the case if the bai has in fact been in place for much longer time than the modelled 10,000 years and/or the loss rate is much slower than 0.001 kg/ha/year used in this simulation, causing accumulation of nutrients in the biomass around the bai. In this case, the observation of increasing concentrations *away* from the bai could be a result of a gradient generated by more recent and more localised mineral deposits to the West of the bai, superimposed on the ancient gradient created by diffusion from the bai itself. Similarly, the humped-shaped relation of sodium concentrations to the distance from the bai could potentially be explained by the presence of a localised source (or sources) of this mineral somewhere near the middle of the Main Trail. Without comparable data on soil concentrations in the forest, it is not possible at present to identify which of these hypotheses may be true.

The possibility that the bai may not be in fact a significant source of minerals in Langoué, if confirmed, opens up more questions. Why would elephants travel long distances to the bai, and once there, spend most of their time drinking water from water holes, given that water sources are very common in the forest, and the time spent in the bai is time not spent foraging? Klaus *et al.* (1998) found that around one third of the small bais in the Hokou area in Dzanga National Park contained lower concentrations of Na, Ca and/or Mg than forest soils. The authors propose that other reasons for geophagy at bais may include self-medication: high clay-rich soils might relieve the symptoms of diarrhoea related to bacterial or parasite infections. Similarly, clay-rich soils may absorb toxic secondary plant compounds such as tannins and alkaloids present in high concentrations in leaf-based diets. This may improve plant digestibility and help relieve stomach upsets.

These hypotheses do not explain, however, the behaviour observed for elephants at Langoué, where they do not eat soil but rather spend their time pumping air into water holes and drinking it afterwards (Momont, 2007). This suggests that it is some compound dissolved in the water that attract elephants to the bai, and not so much the soil. The water itself is also unlikely to be the reason for visiting the bai, as alternative water sources are abundant throughout the forest.(Blake & Inkamba-nkulu, 2004). Whatever is the substance that attracts the elephants to the water holes, it must be a precious resource, as it promotes guarding behaviour and access to water holes is determined by social hierarchy (Momont, 2007). Further studies may be needed to identify what substances are sought after by elephants in those bais where nutrient amounts are not elevated above the background forest levels.

Relationships with elephant trails

No significant relationships with distance from trail, or the localised density of trails, were identified for nutrient concentrations in litter, indicating little support for the hypothesis that mineral concentrations decrease with increasing distance from elephant trails, or with decreasing trail density. For soil, a significant negative relationship with distance from trail was identified for concentrations of magnesium, as predicted by the hypothesis. Whilst intriguing, this result should perhaps be

interpreted with caution, as the number of data points for soil, and range of distances from trail that were considered, were both limited. Further processing of collected samples could help to validate this pattern.

The general absence of a strong signal suggests that the location of trails may be too dynamic to create a lasting imprint on the distribution of nutrients, which is consistent with the assumptions of the Lateral Diffusion Model. Alternatively, the indices used in this study may not have captured the signal well. It is considered quite likely that the 'Transect Width Score' index was a poor indicator of the density of trails for any single sampling site, as the number of trails crossed between different sampling points on a single transect was rarely uniform. Furthermore, it is possible that the 'Main Trail' is not as important relative to other trails in the area as was initially supposed. There are larger, inter-zonal or long–distance–travel boulevards around Langoué Bai, but they were not accessible during the time of the study due to high elephant activity. These may be a more appropriate focus for future study, which could also consider a greater range of distances and examine soil in greater detail.

Relationships with other predictors

Significant relationships with distance from the closest tree were identified for concentrations of both Na and Ca in litter. Individual trees are known to create micro-spatial gradients in relation to the distance from the trunk in a number of important ecological variables, including soil water permeability (Chandler & Chappell, 2008), pH (Eldridge & Wong, 2005; Zinke, 1962), nutrient concentrations (Døckersmith, Giardina, & Jr, 1999; Rhoades, Jr, & Clark, 1994; Zinke, 1962), electrical conductivity (Eldridge & Wong, 2005), amount of organic matter (Rhoades et al., 1994), and the microbial and faunal biomass of decomposer communities (Kaneko & Kofuji, 2000; Scheu & Poser, 1996). Any of these gradients may impact on the decomposition rates, and root adherence to litter layer may directly increase the mineralisation rates of certain minerals (Gallardo, 2003). These gradients can be tree-species specific and have differential effects on various minerals (Gallardo, 2003; Koch & Matzner, 1993). The significance of this influence, when considered alongside larger scale gradients such as the distance from bai, suggests that a

substantial amount of local variation in mineral content may be due to fine-scale tree-driven processes. Such processes could contribute to the residual variance of broad scale models, such as the Wolfe et al. (2013) Lateral Diffusion Model, making it more difficult to accurately estimate the models parameters from empirical data.

Significant negative relationships with increasing soil moisture were identified for potassium and magnesium concentrations in litter. The direction of these relationships is intuitive, as loss rates of soluble minerals can be expected to increase with water levels or fluxes. A study of leaf litter solubility across 41 tropical woody species found that on average 100% of K, 28% of Na, 21% of Mg, and 4% of Ca in leaf litter were water-soluble (Schreeg, Mack, & Turner, 2013). Consistent with this finding, studies of litter decomposition in tropical forests indicate that 80% of K is released within just one to two months from leaf-fall, whilst the rate of Mg and Ca release is much more correlated with the rate of organic matter decomposition, and, depending on the forest, may take from a few months to several years to fully decompose (Anderson et al., 1983; Bernhard-reversat, 1972; Burghouts, Van Straalen, & Bruijnzeel, 1998; Cuevas & Medina, 1988; Zheng, Shanmughavel, Sha, Cao, & Warren, 2006). Generally, the pattern of litter element mobility found in these studies is K>>>Mg>Ca, although sometimes Ca is released faster than Mg. Sodium, as a non-essential plant element, is not commonly reported in studies on litter decomposition, but one study that did measured it found an increase in Na to more than twice the initial concentration over the course of 8 months of litter decomposition, perhaps due to immobilisation by decomposer microfauna (Anderson et al., 1983). The relationships identified here are congruent with previous studies in that: potassium, as the most soluble of elements, is related only to soil moisture; magnesium concentration decreases with moisture but is also related to a further variable that is encompassed by distance from the bai; and calcium, as the least-soluble element, is not significantly related to soil moisture at all.

In the case of magnesium concentrations in soil, a positive relationship with increasing moisture content was identified, but only when the index of trail density rather than the distance from main trail was also considered. This susceptibility to the inclusion in the global model of terms that were themselves not significant, hints at a lack of robustness of the modelling approach for this dataset. This is perhaps due to

the limited number of samples for soil, relative to the number of parameters in the global model, and could potentially be addressed by the processing and inclusion of further soil samples.

Limitations and future directions

This study could have been significantly improved by measuring and comparing the amount of exchangeable cations in samples collected from the forest soil and from the geophagical soil from the bai. This will be the next step, and more bai samples are currently being collected. With this data it should be possible to resolve the question if there is a significant difference in mineral concentrations of underlying soils between these two habitats.

Another improvement to this research would be the analysis of freshly fallen litter from litter traps rather than collecting litter from the ground. This would control for variation in mineral concentrations due to different stages of decomposition, and it would permit the estimation of the amount of litter fall specific to the site. The robustness of the conclusions reached from this study could be improved with wider spatial sampling, either of randomly distributed points or points in transects along multiple major trails. In particular, sampling along big, long-distance, and likely very old boulevards in the North of and South of the Bai would be the best places to reveal the effects of trails on nutrient distribution, if indeed there are any.

There are also ways that the study could be altered to better assess the importance of trails on the distribution of nutrients in landscape. First of all, the potential relationship between proximity to the Main Trail and magnesium concentration in soil merits further investigation based on a larger number of samples collected at different distances from the Main Trail. Second, the impact of the largest of trails –the long–distance–travel boulevards, which are known to present in the North and South of Langoué Bai, should be assessed. Such boulevards can reach widths much larger than the local boulevards (such the Main Trail), and are likely very old and most permanent, as they tend to follow topographical features and connect distant sites of importance to elephants that stay in place for long times, such as bais (Blake & Inkamba-nkulu, 2004; Vanleeuwe & Gautier-hion, 1998).

A better way to evaluate the possible importance of trail density on nutrient location at a single site could be to map all the trails within a given radius from that point. This would allow the computation of an index such as area occupied by trails within that radius, which could better characterize the relationship between trail density and nutrient concentration. An important problem remains, however, in that different trails are likely of different importance to elephants. A monitoring of use of selected trails of different sizes, for example with camera-traps, would be instructive to describe the dynamics of elephant trails and to identify reliable measures of trail use by elephants.

A study aiming to quantitatively test of the Lateral Diffusion Model in Langoué would need to be of a much greater scope than the present research. In order to generate a testable hypothesis, it would require accurate parameterization with actual values for all abiotic inputs and losses, mineral concentrations in the bai as well as characteristics (biomass, size, ranging behaviour) of all herbivore species in the community. It would also need fine-tuning to account for the fact that mineral intake from the bai is in the form of mineral-enriched water and/or soil, and less from edible biomass. The location and mineral concentrations at other mineral deposits within the forest should also be mapped and accounted for.

Other places where the fertility gradients are better characterised than in Langoué may be in fact better suited to test this model. These could include gradients in nutrients created by large alluvial planes, or inland gradients in sea-salts. In the absence of animal-mediated diffusion both would be expected to create sharp boundaries in soil fertility and nutrient concentrations in plants, but a spatial gradient of nutrient concentration in plant tissues would be expected if animals diffused nutrients across the boundary. The advantage of these gradients is that they are likely to be large enough to test on the regional or continental scale that the model is best suited for (as it ignores other sources of variation that can be important on smaller spatial scale). However, the difficulty may be in finding such places where the large mega fauna still persists at natural densities and where its movements are unobstructed by human infrastructure.

Perspective

Testing a hypothetical model in a real, complex ecosystem is a challenging task. The application in this study of the Lateral Diffusion Model – which was conceived to describe patterns over large spatial and temporal scales - is based on the assumption that the bai is the single source of the studied minerals in the landscape. As this study showed, however, nutrient concentrations can be variable at small spatial scales and may be substantially influenced by a host of environmental and biotic variables that are likely to be spatially structured, but are not accounted for in the model.

Although this study focused on nutrient dispersion in a Central African forest, where the forest elephant is the most important of all animal dispersers, it aimed to test a general model of herbivore dispersion of nutrients that should be widely applicable. With the exception of Africa, most of the Pleistocene mega fauna has disappeared before the onset of human civilisation (Barnosky et al., 2004), and more species, such as aurochs (*Bos primigenius*), tarpan (*Equus ferus ferus*) and wisent (*Bison bonasus*) have been driven to extinction in Eurasia in recent centuries (Pretorius et al., 2011). Thus, if the Lateral Nutrient Diffusion model is correct, most of the nutrient diffusivity potential due to animal transport has been lost already in large parts of the world (Doughty, Wolf, & Malhi, 2013; Wolf, Doughty, & Malhi, 2013). Now the double sword of progressing defaunation combined with proliferation of roads and expansion of human infrastructure is threatening this ecological function even further, especially because large animals tend to be extirpated first from the ecosystems (Canale, Peres, Guidorizzi, Gatto, & Kierulff, 2012; Galetti & Dirzo, 2013; Phillips, 1997; Poulsen, Clark, & Palmer, 2013). The consequences of the loss of this function may not be as apparent in the short-term as for example the loss of seed dispersal function, but is set to change the course of the evolution of ecosystem structure and function over millennia (Galetti & Dirzo, 2013; Terborgh, 2013; Wolf et al., 2013). Even though conclusive results have not been achieved in this study, Lateral Diffusion model merits further research to test its power to predict the affects of herbivore communities on nutrient distribution .

6. Conclusion

The Lateral Diffusion Model of Wolf et al. (2013) offers significant novel insights into our understanding of the forces governing spatial patterns of fertility, and how those are being affected through defaunation and restricting the movements of large mega fauna, but remains untested empirically. This study was a first attempt to test the hypotheses generated by this model, as well as the possibility that animal paths create an imprint on the spatial distribution of minerals. An unexpected result — that concentrations of three out of four minerals decrease with proximity to bai — challanges the initial assumption that the bai is the most important source of these minerals in the studied landscape, which generates new questions about the role of the bais in the forest elephant ecology. The importance of trails for nutrient distribution was not evident except for tentative support from the distribution of soluble-soil magnesium. However, it merits further studies, particularly on the largest and most permanent of trails – the long-distance travel elephant boulevards.

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