Adding space-based vegetation structure measurements to a global ecosystem model to simulate tropical forest animal communities and their role in ecosystem function

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Introduction

Animal biodiversity is currently under great threat partially because there are currently no global-scale datasets available to help inform policy decisions, especially in tropical forest regions (Dirzo et al 2014). Satellite data has global coverage but such data has rarely been used to help preserve animal biodiversity. Local-scale studies have shown a wealth of ways in which animals provide ecosystems services (e,g, carbon cycling –Figure 1). However, there is currently no way to upscale how these services cascade through entire ecosystems, especially in data limited tropical forests. A macroscale mechanistic understanding of the roles animals play in tropical forests would be invaluable.

Recently there has been an explosion of satellite derived data that can be used to address many of the world's most pressing environmental problems. We are now on the verge of global LiDAR coverage and a new spaceborne LiDAR will be installed on the International Space Station in Nov 2018—the Global Ecosystem Dynamics Investigation (GEDI) (Qi and Dubayah 2016) (Co-Investigator Goetz is the GEDI Deputy PI for Science, and co-Is Jantz and Burns are members of the GEDI Science Team). This will dramatically increase the geographic extent (51.5° S to 51.5° N) over which habitat structure can be systematically measured. Here we propose to use this explosion of new satellite data and especially GEDI, to help explain the valuable roles animals play in forest ecosystems thus prioritizing biodiversity conservation in tropical forests, the most data limited region of the planet.

We propose to combine this new global forest structure data with a General Ecosystem Model (GEM), the Madingley model (Harfoot et al 2014), which can address the link between animals and ecosystem processes on a global scale. Rather than modelling individual species, our model instead combines animals into cohorts based on their functional traits, including trophic level (herbivore, omnivore, and carnivores), reproductive strategy (semelparity vs. iteroparity), thermoregulatory mode (endothermy vs. ectothermy) and mobility. These traits are used to determine the nature and strength of interactions that modelled organisms engage in. Mass scaling relationships then determine how total biomass of plants, and animal mass in relation to optimal prey size determine the rates of ecosystem processes. The Madingley model has accurately predicted emergent ecological patterns such as individual growth patterns, community rates of biomass turnover, ecosystem trophic pyramids, and macroecological global patterns of trophic structure (Harfoot et al 2014 and Bartlett et al 2016).

Canopy structure derived from LiDAR data can be used in conjunction with modern bio-logging devices (Wilmers, et al 2016), to assess the landscape attributes that motivate the movement behavior and interactions with other species. Bio-logging involves the use of remote sensors that can continuously measure most aspects of an animal's state (e.g., location, behavior, caloric expenditure, interactions with other animals) and external environment (e.g., temperature, salinity, depth). Modern technology, such as accelerometers sampling at 16hz or faster, can be used to well determine the behavior of individual animals (Wilmers, et al 2016) and how that may vary as a function of lateral and vertical canopy structure.
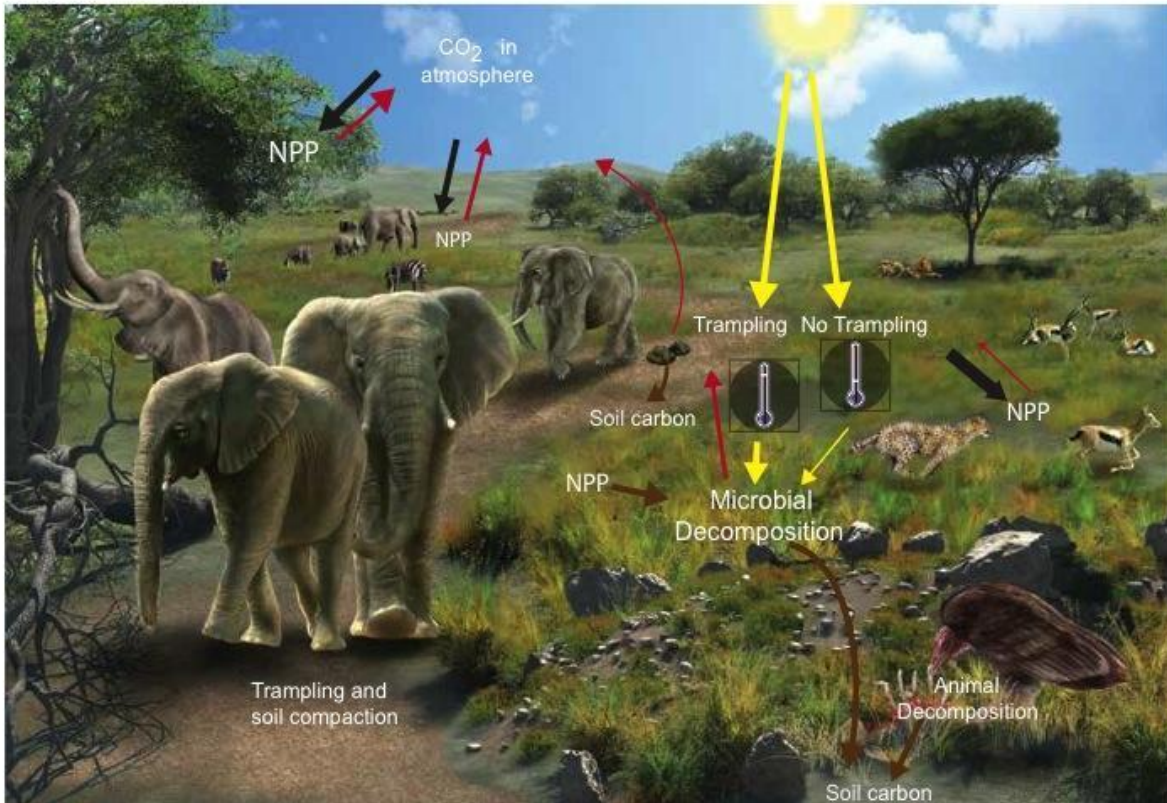

Figure 1 The many ways that animals can affect ecosystem carbon cycling. Animals can mediate uptake (black arrows) and release (red arrows) of CO_2 thereby determining levels of net primary production (NPP) by influencing the amount of plant biomass present in an ecosystem through browsing and tree damage (elephants in foreground), and through grazing (herbivorous animals in left background). Predators can influence herbivore impacts on NPP by reducing their spatial abundance via predation and by causing prey to forego foraging to evade predation (right foreground). Animals can further influence biophysical conditions such as temperature and soil compaction through destruction of vegetation or trampling that in turn alters local rates of NPP and decomposition. Animals can determine the amount of organic matter biomass and chemical elemental quality of that biomass in NPP that enters the soil pool (brown arrows). Animal egestion and excretion, and decomposition can lead to net soil uptake of carbon. From Schmitz et al in review.

Recent empirical studies have shown how many groups of animals interact with and affect vertical tropical forest structure. However, these new studies have not yet been incorporated into large mechanistic models. Near-global LiDAR (GEDI) now gives us the ability to simulate animal/forest interactions at a large scale. Below, we will give a short overview of some of this work that forms the empirical basis for our modeled upscaling. For instance, recent work has combined animal GPS tracks with LiDAR data to show how tropical forest animals use vertical tropical forest structure (McLean et al 2016). Next, large tropical mammals such as forest elephants have large influences on tropical forest structure and recent empirical studies have quantified some of these aspects. Insects play a large role in tropical forest herbivory, but until recently, this had not been quantified. Humans can also impact how animals move and use space. Finally, how tropical forest animals move and use space affects important ecosystem services like seed and nutrient distribution. We first show recent empirical advances and then will detail how we plan on incorporating all these results in to a state of the art global mechanistic model (Madingley) in combination with GEDI and MODIS data.

Arboreal tropical forest animals use of vertical space

The canopy of forests host great arboreal mammal diversity. For instance, over 75 % of all vertebrates and 60 % of mammal species occupy neotropical forest canopies (Kays and Allison 2001; Malcolm 2004). We are just now beginning to understand mechanistically how such mammals use the forest canopy. Arboreal mammals prefer canopy features that aid movement and provide foraging resources (Davies and Asner 2014). Mature forests often provide the most
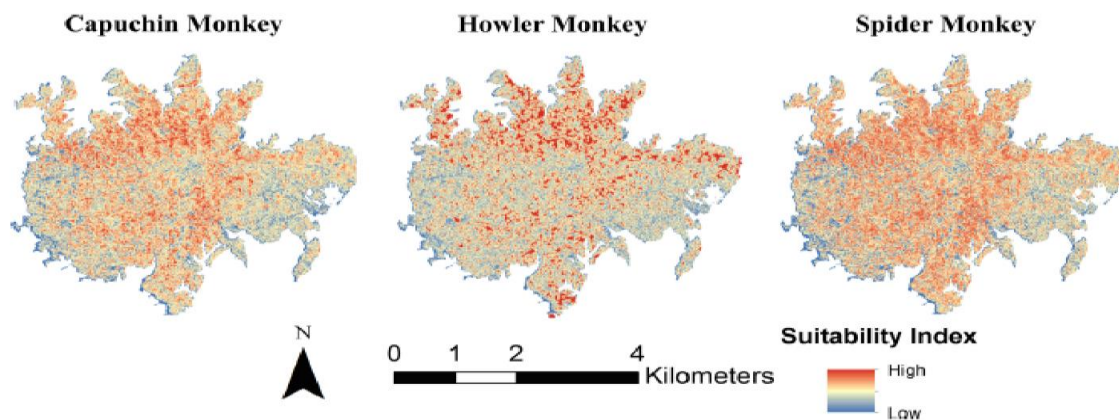

Figure 2 – Maps of suitability of the canopy on Barro Colorado Island, Panama, as predicted by step selection function (SSF) models that related movement trajectories to LiDAR-derived measures of forest structure for three focal primate species. Colors indicate high (red) and low (blue) suitability. From McLean et al 2016

suitable habitat for arboreal fauna, particularly in the Neotropics. For example, tall canopies—a proxy for forest maturity—were a strong predictor of habitat use by Bald-faced saki monkeys (Pithecia irrorata) in the Peruvian Amazon (Palminteri et al. 2012). Another example of three monkey species from Panama is described in Figure 2 (McLean et al 2016).

These arboreal seed dispersers have large implication on biodiversity and ecosystem services such as carbon sequestration (Harrison 2011 and Young et al 2016). How seeds are distributed depends heavily on the movements of arboreal dispersers (Russo et al. 2006), but

understanding these movement patterns requires mechanistic models for predicting how species move through the canopy (Muller-Landau and Hardesty 2005). For instance, recent work showed that forest ecosystems stand to lose 66% of their carbon storage capacity following the loss of trees dispersed by large bodied frugivores (Bello et al 2015). Similarly, losses of frugivorous primates throughout the Amazon forest, which also control seed dispersal and tree recruitment, can cause an estimated 2.5% - 5.8%, loss of carbon storage potential in tree biomass, and could reach as high as 26.5% - 37.8% (*Peres et al 2016*). Therefore, we plan to use arboreal animal bio-tracking data, and global LiDAR to incorporate how arboreal animals use space to better estimate their important ecosystem services.

Forest elephants as Ecosystem engineers

Size class	No. of trees Perú	No. of trees Gabon	Number of tree species	
			Perú	Gabon
No. trees/species	2383	2383	448	283
>60 cm dbh	59	185	43	70
>50 cm dbh	101	284	65	89
>30 cm dbh	370	794	166	162
<30 cm dbh	2013	1589	282	121

Table 1- Individual trees and tree species in different diameter classes in composite samples of 2383 trees from 6 Peruvian and 6 Gabonese terra firme forests. From Terborgh et al 2016.

Forest elephants are ecosystem engineers much like their larger savanna cousins (Asner et al 2016). They are under even greater threat and their numbers have been reduced drastically in the past decades (Maisels et al., 2013). Much current research is just beginning to highlight how forest elephants influence other vegetation processes such as forest carbon cycling (Omeja et al., 2014; Terborgh et al., 2016a). One interesting hypothesis is that the presence of megafauna in African tropical forests, as opposed to Amazonia where fewer large herbivores species remain, might contribute to the differences in structure and above ground biomass (AGB) between the two regions (Lewis et al., 2013; Terborgh et al., 2016b). For example, the presence of megafauna might account for some of the differences in structure and composition between Gabonese and Peruvian forests (Table 1) (Terborgh et al., 2016b). Forest elephants, by clearing the understory and increasing tree mortality within certain size classes, might be partly responsible for the lower stem density (425 stems/ha) and higher mean tree size (0.074 m²) and AGB (429 Mg/ha) of Central African compared to Amazonia forest (597 stems/ha, 0.049 m², and 341 Mg/ha) (Lewis et al., 2013). Other studies have also speculated that a reduction in forest elephant disturbance following their population collapse, may partly contribute to an increase in above-ground carbon storage in African tropical forest (Lewis et al., 2009, 2013).

However, this hypothesis has not yet been tested mechanistically regarding the role of megafauna. To address this research gap, we propose to input the role of megafauna on forest structure in the Madingley model. We hypothesize that by reducing the number of stems, this thinning process might lower the competition for resources (light, water, and nutrients) among plants and allow larger and older trees to dominate (Lewis et al., 2013). LiDAR is an effective tool for helping to understand elephants' impact on forest structure. Elephants have been shown

to be the dominant driver of treefall in African savannas using on-the-ground data on African elephant densities and LiDAR-derived measurements of woody vegetation (Asner et al 2016 and Davies and Asner, forthcoming). Savanna studies have shown that the effects of bull elephants are landscape dependent, leading to decreases in carbon along rivers, at mid-elevations, and on steeper slopes. We have access to high resolution LiDAR data for large areas of Gabon, home to some of the highest populations of forest elephants in the world. We plan to use this data, plus on the ground elephant density data to understand how ecosystem engineers like forest elephants impact forest structure. We will combine this empirical understanding then will incorporate this knowledge into the Madingley model as an ecosystem engineer cohort.

Insect herbivory in tropical forests

Insects play a vital role in carbon cycling in tropical forests, but there is little data and fewer mechanistic models to understand thi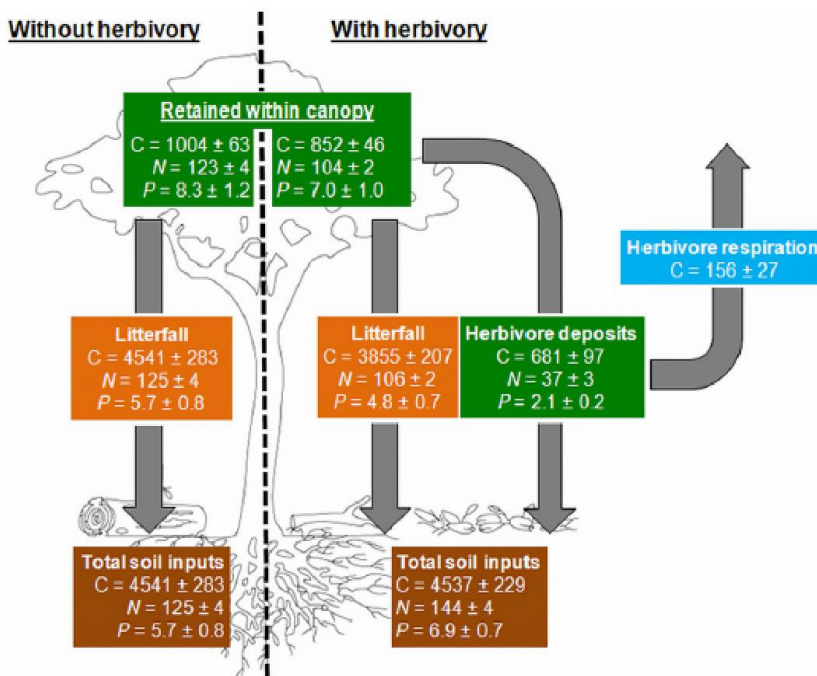s process (Coley & Barone 1996). Insect herbivore-mediated processes can impact the quantity and quality of organic material transferred to the soil, and/or plant species composition, with variable net consequences for soil processes depending on the herbivores and ecosystem in question (Bardgett & Wardle 2003). In general, deposits from insects (excreta, bodies, unconsumed leaf fragments) were relatively labile: decomposing more rapidly than plant litter (Fonte & Schowalter 2004), increasing levels of soil N and P, and driving a variety of shifts on soil organic matter cycling (Fonte & Schowalter 2005). A recent study quantified the magnitude of, and

Figure 3 Carbon, nitrogen and phosphorus fluxes of lowland Amazon forest with and without invertebrate herbivory. Values represents means ± SE ($n = 2$), in units of kg ha^{-1} year^{-1}, calculated from the two lowland forest plots in this study. Herbivore deposits represent the sum of excreta, moults, bodies and unconsumed leaf fragments. From Metcalfe et al 2015

underlying controls on, carbon, nitrogen and phosphorus cycled by invertebrate herbivory along a 2800 m elevational gradient in the tropical Andes. The results indicate that leaf area loss is greater at warmer sites with lower foliar phosphorus, and secondly, that the estimated herbivore-mediated flux of foliar nitrogen and phosphorus from plants to soil via leaf area loss is similar to,

or greater than, other major sources of these nutrients in tropical forests (Metcalfe et al 2015). This study found that herbivores consume a significant portion of plant carbon, potentially causing major shifts in the pattern of plant and soil carbon cycling. We propose to use these insect herbivory results, along with new datasets currently being generated (see below for details), plus LiDAR-derived forest structure data to better incorporate how tropical insects consume leaf NPP with vertical structure.
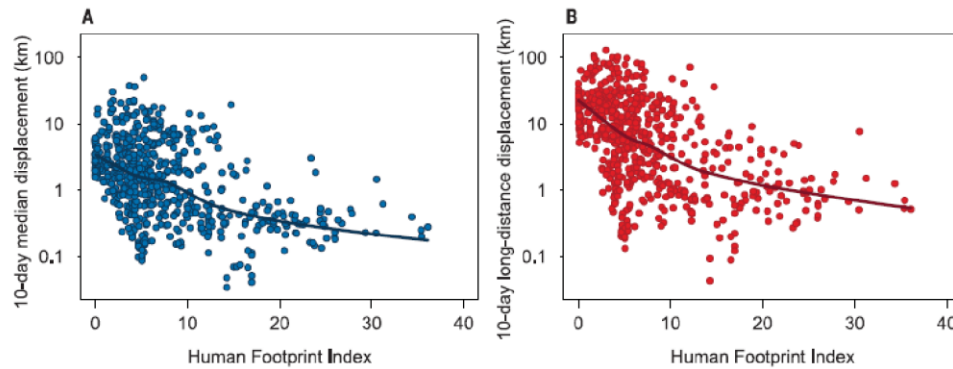
Humans modify animal use of space

Figure 4 – Mammalian displacement in relation to the Human Footprint Index. (A) Median displacements; (B) long-distance (0.95 quantile) displacements. Both displacements decline with increasing human footprint (n = 48 species and 624 individuals). From Tucker et al 2017

Recently, a paper in *Science* has demonstrated that humans can significantly negatively impact animal use of space (Tucker et al 2018). Specifically this paper used a GPS-tracking database of 803 individuals across 57 species, and found that mammal movement decreased by half to a third in areas of high human footprint in comparison to those with low human footprint. This was attributed to behavioral changes of animals to avoid areas with high human footprint.   This paper found mathematical relationships between human footprint and animal movement that can be incorporated into Madingley. Since animal movement greatly impacts key ecosystem process such as predator-prey interactions, nutrient cycling, and disease transmission, it is important to have predictive modelling of these traits. We propose to incorporate these results into Madingley by having a human footprint dataset impact animal movement and ecosystem services.

Ecosystem services provided by animals
Two recent studies compiled size relationship data for terrestrial mammals within a random-walk mathematical framework and found that the distribution of nutrients away from a concentration gradient is size dependent (with a scaling exponent of 1.17) suggesting that larger animals are disproportionately important for the flow of nutrients (*Doughty et al 2013 and Wolf et al 2013*). These papers used modern mammal species range maps and body mass to globally estimate the ability of animals to transport nutrients as a diffusivity (or the ability of nutrients to move away from a nutrient concentration gradient, just like thermal diffusivity indicates the ability of a surface to move heat away from a hot area) in units of square kilometres per year (*Doughty et al 2016*). Extinctions and hunting pressures over the past 12,000 years decreased this nutrient

diffusivity by large animals to less than 10% of its former value (*Doughty et al 2016a*) leading to significant hypothesized decreases in nutrient concentrations at the continental scale (*Doughty et al 2013 and Wolf et al 2013*). This framework could be easily incorporated into the Madingley model. Therefore, with LiDAR 3D structure we will show how animals move through vertical space and in this component we will show how they provide ecosystem services.

In this proposal, we will specifically address the following Sustainable Development Goals (SDGs):

Target 15.5 • Take urgent and significant action to reduce the degradation of natural habitats, halt the loss of biodiversity and, by 2020, protect and prevent the extinction of threatened species

Target 15.9 • By 2020, integrate ecosystem and biodiversity values into national and local planning, development processes, poverty reduction strategies and accounts

In tropical forests, animals move nutrients and impact carbon cycling. With Madingley, these services can for the first time be quantified and provide impetus across entire ecosystems to better preserve local biodiversity, thus preventing their extinctions. Because we envision this to be a pan-tropical tool, these services can also be integrated into national and local planning. Animals that contribute to accelerated carbon sequestration could be incorporated into REDD+ and SDG frameworks, leading to possible poverty reduction as well as co-benefits of reducing forest loss and increasing biodiversity preservation. In addition, Madingley will calculate many key essential biodiversity variables (EBVs) such as those listed in figure 6. Such pan tropical EBVs will provide much data to help specific partner countries preserve their biodiversity. We will leverage co-I Goetz and Jantz's participation in an ongoing project funded by the Ecological Forecasting program that is partnered with the UN Development Program to address *Forest Integrity for Conservation Planning*. That effort provides unique access to in-country partners and participants engaged in reporting on progress towards achieving SDGs, including SDG 15.5 and 15.9 to which this proposal is most relevant, in Brazil, Gabon and Peru.

Specifically, in this proposal we will include the following tools:

1. ***Time series of satellite remotely sensed data*** – We propose to drive Madingley with MODIS GPP and NPP, which will inform available plant energy that animals in tropical forests can consume. These products are not perfect for tropical forests (see Cleveland et al 2016), but our group has extensive experience with tropical forest GPP and NPP (see Doughty et al Nature 2015 as an example) so we can modify these with available field data where available. We will combine this with LiDAR canopy structure data products from GEDI and airborne lidar (where available) which can provide full 3D characterization of habitat, including vertical profiles of cover, biomass and carbon density and foliage height diversity (*Goetz et al 2015 and Tang et al 2017*).
2. ***Time series of in situ biological observations*** - We will use ground based bio-tracking data from the tropics to inform Madingley such as GPS and accelerometer data for animals from

the Atlantic and Amazon forests in Brazil (with Co-I Riberio) as well as forest elephant density data from Gabon.

3. *Use of ecological models* - We will improve the only global ecological model (Madingley) capable of producing pan-tropical country specific estimates of key EBVs and carbon cycling parameters. We will also use simulated tropical forest NPP from NCAR's CESM CLM model to run Madingley under future potential climate change scenarios. Doughty currently has both models running (CESM on NAU supercomputer Monsoon, and Madingley on a high performance desktop).
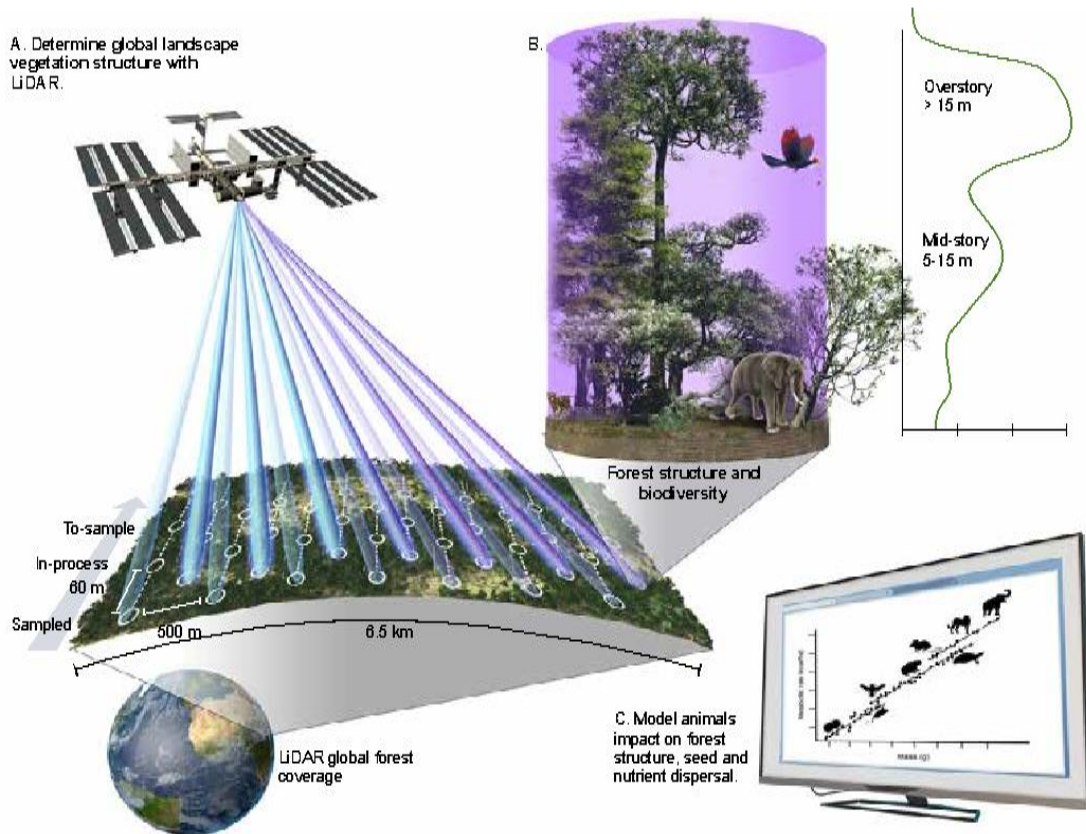

Figure 5. Potential future methods of detecting and predicting how animals impact their environments. (A) Satellite derived LiDAR data that can predict global forest structure. (B) A hypothetical scene where LiDAR detects elephant driven changes to forest structure. Alternately, LiDAR data predicts forest structure that indicates habitability by certain bird species. (C) Hypothetical global ecosystem model predicting animal driven changes to forest structure, seed dispersal, and nutrient dispersal using mass based scaling equations. From Schmitz et al in review.

We propose to add five new animal functions to the Madingley model

1. Arboreal cohorts that can make use of vertical tropical forest structure based on GEDI data and Brazil arboreal animal GPS and accelerometer data
2. Ecosystem engineer cohort based on Gabon high resolution LiDAR data and forest elephant data.
3. Insect consumption of vertical tropical forest NPP using Peruvian insect dataset.
4. Animal movement can be constrained due to the human footprint
5. Add ecosystem services by animals such as nutrient distribution to Madingley

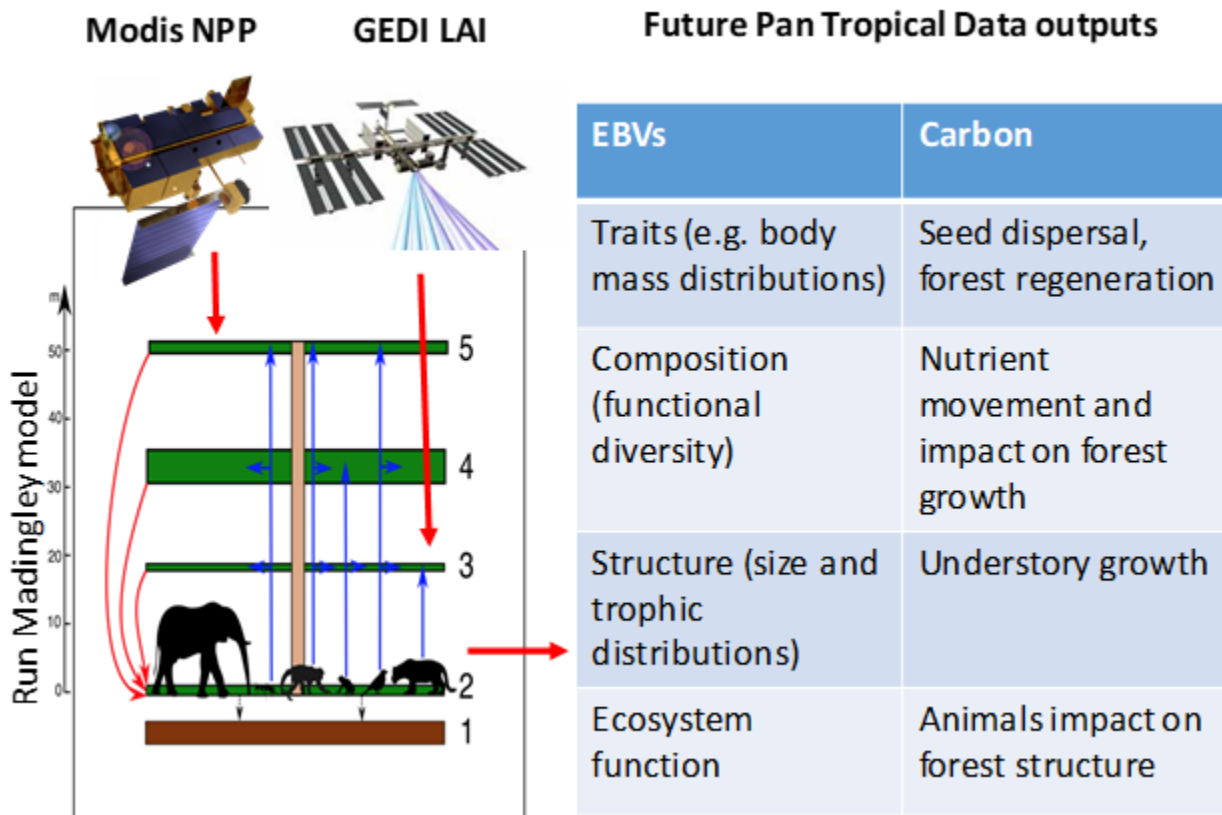| EBVs	Carbon
Traits (e.g. body mass distributions)	Seed dispersal, forest regeneration
Composition (functional diversity)	Nutrient movement and impact on forest growth
Structure (size and trophic distributions)	Understory growth
Ecosystem function	Animals impact on forest structure

Figure 6 – Using Modis and GEDI data we will drive the Madingley model and add new animal cohorts to make use of this vertical structure. Based on these changes, we will then produce a number of EBVs and Carbon cycling data outputs (right) that could be used by tropical countries to inform policy decisions.

Overall

"The grand challenge is to put all these pieces of information together into a global framework that can help us understand the biosphere as a system and how and why it is changing."

Animals are an often neglected in efforts to understand the biosphere as an integrated system. We believe that by improving Madingley with forest structure data and testing it with a number of empirical datasets we can better understand the biosphere as an integrated system. Animals

are not just passive recipients of nutrients and energy, but actively drive ecosystem dynamics. We have shown the many ways in which animals can control and alter their ecosystems across broad landscapes. Consequently, animals and their functional roles should be considered as part of the biosphere but currently they are not. Indeed, disregarding them could lead to serious inaccuracies in models, as well as lead to ineffective policy formulation and management efforts. Our proposal, if funded will start to address these issues.

Methods

The Madingley model, the only current model capable of providing global animal EBVs and ecosystem services for all animals at the community level, currently acts like figure 7a, where all animals have equal access to plant NPP. This is obviously not correct, a significant limitation of the model.   If funded, our goal is to have Madingley predict accurate ecology, trophic interactions, EBV's, and ecosystem services for the pan-tropics similar to figure 7b and 7c. and with Modis NPP to determine real time available plant energy and GEDI to provide vertical structure.

The different widths of green vegetation in figure 7b approximates the amount of plant matter available at each level based on the GEDI structure data. For instance, in the below case, GEDI LAI would estimate that most available plant energy is in the canopy, with very little in the emergent layer and understory. In addition, GEDI will estimate horizontal heterogeneity in autotrophic biomass heterogeneity. Therefore, real (large) gap dynamics can impact real time animal ecology. If the canopy changes vertical structure over time, GEDI will detect this and we can predict modified EBVs and ecosystem services based on these structural changes.
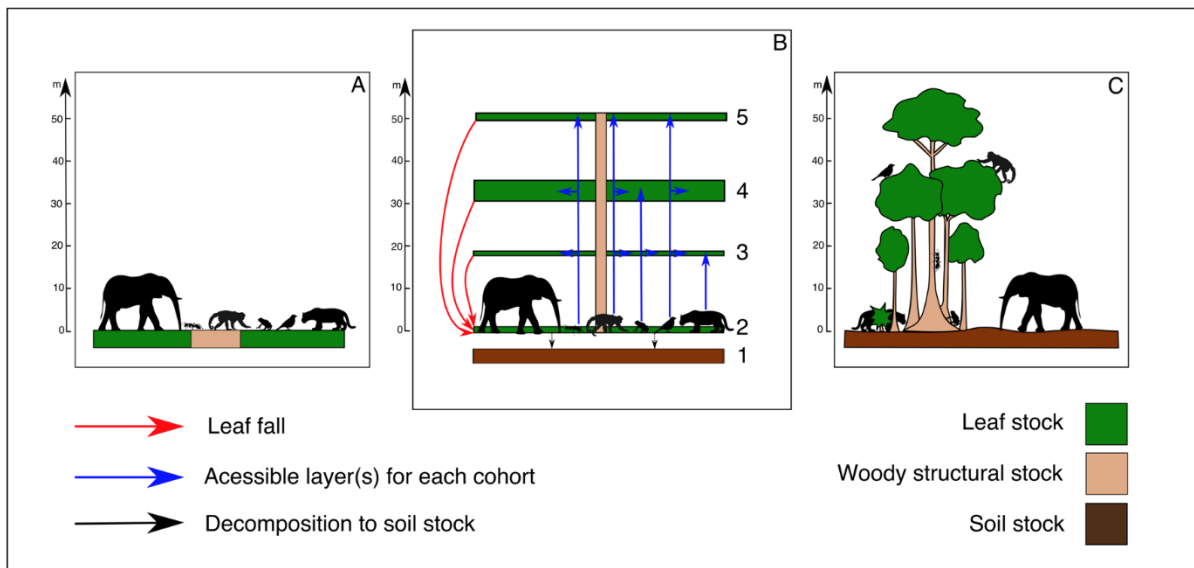

Fig 7. Schematic diagrams of the vertical plant structure in a) the current Madingley model, b) our proposed integration of GEDI LiDAR LAI data in the Madingley model and c) real tropical forests. The numbers in panel B refer to 1) the soil stock, 2) forest floor, 3) understory layer, 4) canopy layer and 5) the emergent layer.

We will then parametrize an animal cohort to use the vertical space matrix based on data from existing species (GPS and LiDAR data from published or case studies). From these, we can create functional groups, which we know the range of vertical vegetation layers over which

they might visit or interact with (e.g. jaguar = forest floor and understory, larger birds = all layers, monkeys = emergent layer or canopy, insects = everywhere but informed by leaf herbivory dataset). Since we don't know the % time spent in each layer for most species, we can at first just split equally (i.e. 25% in each if four layers, 33% for three layers etc), use GPS data where available, or build relationships based on leaf/prey biomass. For instance, insects spend more time in canopy than emergent layer as there is more leaf biomass/prey available.

With this methodology, we can represent the two main reasons animals use vertical structure - food and security. For example, our "monkey" cohorts may spend much of their time in the canopy, which is safe from the "jaguar" cohorts. They will only be available prey during their forages into the lower levels, whilst tapir/white-lipped peccaries will be exclusively feeding from the forest floor. They will therefore be available as prey for the "jaguars" at all times. Capturing these accurate trophic interactions will be key to accurate pan-tropical estimates of EBVs and ecosystem services.

We specifically will incorporate the following three steps to the Madingley model:

1. Use satellite derived MODIS GPP and NPP to quantify real time available plant energy for all tropical forests. We will also use simulated tropical forest datasets from NCAR's CESM CLM model to run Madingley under future potential climate change scenarios.
2. Use GEDI LiDAR to split available plant energy into four accurate vertical bins based on various height thresholds (i.e. 0,1,2,40,50m) as shown in figure 7b. Co-Investigator Goetz is the GEDI Deputy PI for Science, and co-Is Jantz and Burns are member of the GEDI Science Team.
3. Use local field sites from which we have good contacts to run and test Madingley before up-scaling to a pan-tropics. We list these local sites below:

Regional
      a. Gabon - High resolution airborne Lidar data (NASA LVIS from AfriSAR 2016 campaign), forest elephant density (Maisels et al 2014), and impact on forest structure impact (Terborgh et al. 2016).
      b. Brazil - Biosensor data for the Amazon and Atlantic forests (Riberio et al 2011) combined with spaceborne GEDI data.
      c. Peru - Insect herbivory and high resolution carbon cycling data (Metcalfe et al 2015) combined with spaceborne GEDI data.

Global
      d. Incorporate human footprint impact on animal motion based on equations from Tucker et al 2018.
      e. Incorporate global lateral animal nutrient diffusivity maps from Doughty et al 2013 and 2016.

Specific empirical datasets and methodology we will use to parameterize Madingley

Addition 1 – How mammals and birds use vertical space in tropical forests

Importance – Currently there is no vertical structure to vegetation in Madingley and all herbivores have equal access to all leaf NPP.

What we will do – We have created a spreadsheet containing published studies from tropical forests where authors have combined bio-logging data with LiDAR forest structure data (https://docs.google.com/spreadsheets/d/1Vw72Ng72oO_N3dQMoTt97eiv_0-8lz51DMPo4EEE8gc/edit?usp=sharing). We will first analyze these papers and any others we can find to create mass scaling relationships of how animals can access leaf NPP in our four different structure levels. Then, after adding 3D tropical forest structure to Madingley using LiDAR data, we will create a cohort of animals that can make use of the new vertical structure. For instance, we show a figure from McLean et al 2016 (Figure 2) where LiDAR data was combined with telemetry data to show how three different monkey species use space. Based on all our data, we will look for mass based relationships in these datasets and if they exist, add them to Madingley.

However, in our search of this literature, we have found such data with both biosensors and LiDAR data to be very limited. However, project partner Milton Ribero has large numbers of biotracking data such as GPS and vertical accelerometers throughout Brazilian forests (both Atlantic and Amazon). For instance, there is GPS data for Peccaries, Jaguares, Wolves, Foxes, and Pumas and accelerometer data for the Gladiator frog and Golden Lion Tamarins. Other colleagues have also offered to share tracking data (for example, Carlos Peres has white-lipped Peccarie and tapir GPS data for the Amazon).   We will combine this bio-tracking data with the GEDI structure data to parameterize how these species use space. Specifically, project Co-I's Jantz and Burns, will work with Ribero and others on this. Based on these data and the literature search, we will parameterize Madingley on how certain animals use vertical tropical forest space.

Addition 2 – Add ecosystem engineer cohort to Madingley

Importance – Large herbivores are ecosystem engineers with a significant impact on forest structure.

What we will do – We will first use LiDAR data from the Laser Vegetation and Ice Sensor (LVIS) that has already been collected at 18m footprint resolution across Gabon, in coordination with the AfriSAR project. We will use these data to better understand the impact of forest elephants on forest structure. We will then relate this to the less densely sampled 25m forest structure data products derived from the GEDI LiDAR. We have the best available information on forest elephant density that we will relate to the LiDAR structure metrics. Based on these data sets and the Terborgh et al. (2016a) datasets on how forest elephants affect forest understories, we will also add an ecosystem engineer cohort to Madingley that can impact forest structure. For Madingley, this will assume the form of forest dwelling herbivores>1000kg that will impact forest structure. Where this cohort exists, more forest NPP will be distributed throughout the canopy (e.g. shifted to higher layers) based on what the LiDAR data show.

Addition 3 – Add canopy insect herbivory and verify with data from Metcalfe et al.

Importance – Tropical forest insect herbivores consume significant amounts of leaf NPP and nutrients and this can have a significant impact on total forest carbon and nutrient cycling.

What we will do – Madingley already has an insect cohort, but currently this cohort has equal access to all NPP (Figure 7a). We now have available the first pan tropical insect herbivory dataset from Peru, Brazil, Bolivia, Gabon, Ghana, and Malaysia (Doughty is a project partner on this project). As an early example of this work, Metcalfe et al 2015, scanned leaves collected from litter traps in Peru and then estimated percent herbivory. This dataset is almost entirely for insect herbivory because larger herbivores tend to eat the entire leaf. The quantity of leaves eaten was demonstrated to have a significant impact on total leaf area as described in the introduction.

At each site, we have data on total GPP, NPP, LAI, as well as total insect herbivory. Based on these data we know the total consumption of NPP by insects across the tropics. We can then modify the variables for insects (ectothermic herbivores < 50g) until they match the NPP consumption at each of plots.

Addition 4 - Human modification of animal motion

Importance – Madingley currently does not account for potential human impacts on animal movement which could also impact the ecosystem services that they provide.

What we will do – Madingley currently uses mass based scaling to predict movement of animals. We will modify this based on the results from Tucker et al 2018 and shown in figure 4. When animals are closer to humans their long term ranges are smaller. This will affect competition between animals and their well being. We propose to add a parameter reducing animals movement following the equations above in addition to the typical mass based scaling parameters. Specifically, we will input a human footprint map to Madingley similar to that used in Tucker et al 2018 and Venter et al 2016 (Co-I's Goetz and Jantz have access to the HFI dataset). Using the mass-based equations from Tucker et al. 2018, we will introduce a negative weighting factor on animal movement when the human footprint index is high.
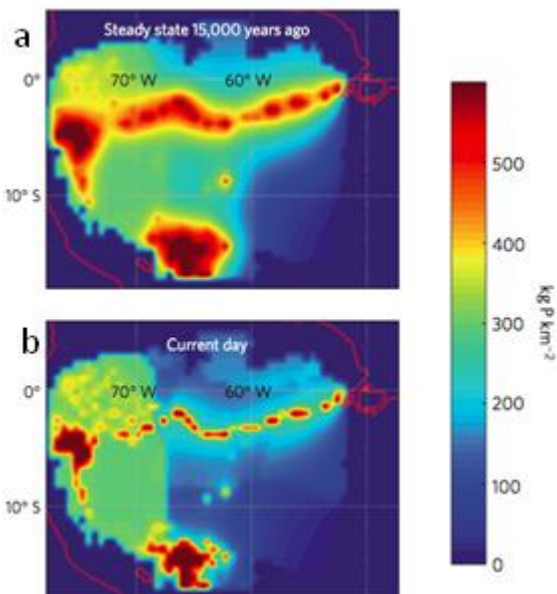
Addition 5 - Calculate lateral nutrient diffusivity for animals

Importance – Animals currently perform a vital ecosystem service of nutrient distribution but this is not incorporated into Madingley.

What we will do – The Madingley model already allows for the lateral diffusion of animals across space and already has mass based scaling parameters. Therefore, the addition of our mass based equations for nutrient movement to Madingley should be relatively straightforward. We also plan

Figure 8 - Estimated movement of phosphorus concentrations in the Amazon Basin (a) with large animals and (b) without. From Doughty et al 2013.

on adding a very simple linear growth parameter to Madingley that will allow for increased plant growth where there are more rock derived nutrients like Phosphorus. Specifically, there will be an underlying global soil map with nutrient concentration gradients and based on our mass based equations, animals will distribute these nutrients across landscapes. Then we will add a small amount of NPP to our satellite derived NPP based on the availability of such nutrients like phosphorus. Therefore, we can capture real time feedbacks between forest structure, nutrient movement, and forest productivity.

Overall

We will first run and parametrize Madingley for individual field sites with changes unique to that particular region. For instance, we will run Gabon just adding the ecosystem engineer cohort using country specific data. Next, once we have confidence that the model results match the local datasets, we will run Madingley for the entire countries of Brazil, Peru, and Gabon with all code changes. We have been in contact with relevant partners from each of these countries to ensure that these countries will have access to the relevant datasets for their reporting needs. Specifically, we will produce EBV's and carbon cycling data listed in Figure 6 for each of these countries in the final year of the three year project. More broadly, after further testing we will eventually provide these datasets for all countries where there are tropical forests and under a range of future potential climate change and deforestation scenarios.

Project management plan – Dr. Doughty will devote a significant portion of his time to ensuring the success of this project and will oversee all components of the research along with the Postdoc. Co-PI Goetz as well as Co-I's Jantz and Burns have extensive experience with LiDAR and will lead GEDI data interpretation. PP Ribeiro will work with Co-I's Jantz and Burns to interpret bio-sensor data. Doughty and the Postdoc, with advice from Harfoot, will lead the incorporation of the results into Madingley.

Task Management plan **-** Participants for each section.

	Doughty	Goetz	Jantz	Burns	Postdoc	Harfoot	Ribeiro
P1– Arboreal movement	X	X	X	X	X		X
P2 – Ecosystem engineer	X	X	X	X	X		
P3 – Insect Herbivory	X				X		
P4 – Human modification	X				X		
P5 – Nutrient movement	X				X	X	
Write up results	X	X	X	X	X	X	X

Risks and mitigation strategies **-** This project depends on existing datasets, published literature, GEDI datasets with knowledgeable participants (Goetz, Burns, and Jantz), and model development with people knowledgeable with the Madingley model (Harfoot and Doughty). Therefore, there is little risk to this project since the datasets already exist, the knowledge on how to use them is within the group and the model is well known to the group. It is relatively low cost considering the breadth of the data that will be produced. Most partners are based at NAU making communication more direct.

*Management plan***-**The project will commence on Dec 2018 on the following schedule:

	Dec 2018	July 2019	Dec 2019	July 2020	Dec 2020	July 2021
P1– Arboreal movement	X	X	X	X		
P2 – Ecosystem engineer	X	X	X	X		
P3 – Insect Herbivory	X	X	X	X		
P4 – Human modification			X	X	X	
P5 – Nutrient movement			X	X	X	
Write up results				X	X	X

Project deliverables **-** We estimate a minimum of five, high quality publications as an outcome of this proposal (one addressing each of the above sections). More broadly, the better parametrization of Madingley for tropical forests will allow us to calculate the EBVs and carbon cycling parameters listed in Figure 6 for all tropical forest countries. Members of our group have had contact with governmental partners in Peru (Michael Valqui - Coordinador Nacional UNDP) and Brazil (Adriana Bayma -Environmental Analyst, Ministry of Environment) at a recent Spatial Data workshop held at WRI last Oct. We are in the process of working with them and others on the best ways to share country specific EBVs and animals ecosystem services datasets. We will leverage co-I Goetz and Jantz's participation in an ongoing project funded by the Ecological Forecasting program that is partnered with the UN Development Program to address *Forest Integrity for Conservation Planning*. Dr. Harfoot has a position at UNEP-WCMC and has colleagues that may provide additional in-country contacts

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