Revisiting the species-area relationship by expanding to the 3rd dimension

Introduction: Habitat loss and fragmentation due to land development disrupt ecosystem services, degrade carbon stocks, and threaten biodiversity[1]. Restoring connectivity between habitat patches is an effective approach to conserve biodiversity in a fragmented landscape, but limited funding requires prioritization of reconnecting habitat patches with high diversity. The theory of island biogeography[2] suggests that area of a habitat patch and amount of space between patches (hereafter the "matrix") are both important for restoration[3]. Consideration of only patch and matrix *area*, however, is inherently a flat perspective: an abundance of life lives above-ground, around 40% of biodiversity in forests[4]. Habitat volume may better predict biodiversity than area, and if so should be an important metric for establishing restoration priorities.

The concept of an ecosystem as a multidimensional space of discrete niches is well-established[5], and although a species-volume relationship has been recently proposed, it has not been rigourously tested[6]. My previous research shows that distinct microhabitats exist in a multidimensional space within forests[7], and evidence suggests that canopy height and structure, which in part determine the number of available niches, influence diversity[8]. Taller, more structurally complex canopies may provide more "vertical niche space" (VNS) for species to use. VNS crossed with patch area can be a metric for patch volume. Some evidence suggests that VNS is more important for determining alpha diversity (hereafter *alpha*) than patch area[9], and high-volume patches (fig. 1B) are expected to maintain higher *alpha* than low-volume patches (fig. 1C). Patch isolation (mean distance to closest patch on all sides) determines how easily organisms can cross between patches, and therefore influences *alpha*[3]. Depending on the land use of the matrix (fig. 1E&F vs. fig. 1G&H), matrix VNS will vary, and high matrix VNS may also increase *alpha* of adjacent patches.

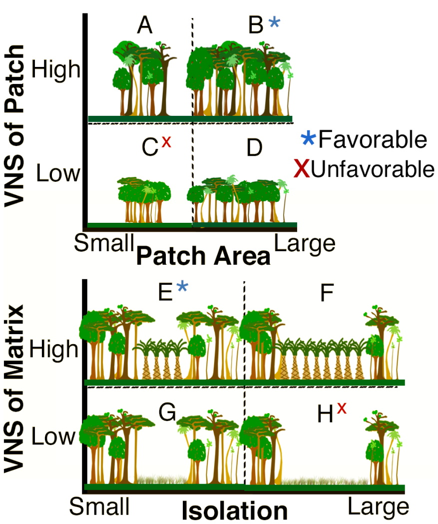

Figure 1. Species-area theory accounts for patch area and isolation (x-axes), but not VNS of patches and the matrix between patches (y-axes).

In regions with immense biodiversity but rapid rates of deforestation, such as Madagascar[10], careful consideration must be given to restoring land between high-diversity patches. Conservation International (a conservation NGO) has scheduled large-scale restoration work in the Ambositra-Vondrozo Corridor (AVC) of Madagascar, but baseline biodiversity and forest cover monitoring is necessary. Herpetofauna (reptiles and amphibians) are particularly threatened both in Madagascar[11] and globally[12]. Herpetofauna are abundant at all forest heights and some species are persistent in even small forest fragments, making them an excellent model taxon to test a species-volume hypothesis. By integrating high-resolution remote sensing of forests from satellites and an unmanned aerial vehicle (drone) with on-the-ground herpetofaunal surveillance, I will test the species-volume hypothesis to inform both ecological theory and restoration efforts.

Hypothesis: I hypothesize that volume of habitat patches and inter-patch matrix more accurately predicts alpha diversity than patch area and isolation distance alone. *Aim 1:* I will determine how well patch area and isolation of habitat patches predict patch *alpha*. *Aim 2:* I will then build upon the species-area theory by evaluating how well patch volume (area crossed with VNS) and matrix volume (patch isolation crossed with VNS) predict patch *alpha*. *Aim 3:* I will use forest structure and patch *alpha* to hierarchically prioritize restoration sites.

Methods: To select sites, I will first use Landsat satellite-derived estimates of forest cover[13] and ICESat LiDAR-derived coarse estimates of canopy height[14], and will calculate patch area and isolation using the SDMTools R package[15]. I will choose sites that are accessible and encompass forest patches that vary in size and structure. To acquire high-resolution models of volume, I will monitor a total of ~84 km^2 (40 days of flights, 0.7 km^2 coverage each) via a senseFly eBee® drone. An equipped CANON Powershot® will record photographs that I will stitch together using Pix4D photogrammetry software to produce 3D orthomosaic point clouds. I will divide the study region into 30m^2 cells and substract orthmosaic points from a digital elevation model to derive mean and variance in canopy height (synthesized into a single VNS index) for each cell[16]. For both patches and matrix, I will multiply VNS by the standardized cell area to calculate volume of each cell. I will record herpetofauna richness and abundance in forest patches across the region by conducting 30 vertical surveys (from forest floor to top of canopy), sufficient for species accumulation (Scheffers, personal communication). I will perform generalized linear models[17] (GLM; pending data structure and distribution) to model *alpha* in relation to 1) the interaction between patch area and isolation and 2) the interaction between patch volume (sum of cell volumes) and matrix volume (sum of non-forest cell volumes within a 5-km buffer zone of a patch). I will then conduct three restoration prioritization analyses using the software Zonation, which will prioritize cells by accouting for desired habitat inputs while iteratively removing the least valuable cells. In analysis (A1) inputs will be patch area and isolation; in (A2), patch/matrix volume; and in (A3) *alpha* of patches. I will contrast site selection for restoration by analyzing the correspondence between output cells from A1 and A2 to cells with high diversity (A3).

Resources: I will be advised by Dr. Brett Scheffers (University of Florida; UF), an expert on Malagasy herpetofauna, I am familiar with single-rope canopy access, and the members of the Scheffers lab are certified with 1,000s of hours of canopy access. I will build point cloud models using UF's HiPerGator 2.0, the world's third fastest university computer.

Intellectual Merit: My proposed research extends a classic ecological theory, the species-area relationship, by combining cutting-edge tools with conventional field methods. If my hypothesis that habitat patch volume can predict diversity more accurately than area is correct, this study will contribute to *Understanding the Rules of Life*, one of NSF's 10 Big Ideas, and my workflow will establish an efficient pipeline for estimating biodiversity. Once such drone methods are achievable via satellite, my study can be replicated without any site visitation. My diversity monitoring may also contribute novel data on critically endangered and data-deficient species[11].

Broader Impacts: My work will inform the ambitious forest restoration projects planned for the AVC (2019-2024) and I have communicated with Conservation International to monitor sites of mutual interest. Forest restoration will enhance ecosystem services, absorb carbon emissions, and mitigate flooding of local communities, and my forest structure data can be used to quantify carbon stocks for offsetting projects in the region. As part of USAID PEER funding (2017-2021) to Dr. Brett Scheffers, we will collaborate with a Malagasy graduate student to train communities to monitor on-the-ground carbon stocks, thereby assisting them with active protection of their forests. I will also facilitate a letter exchange between Malagasy students and the Riverside Elementary School in the US, with which I have established contact on the matter.

Citations: [1] Foley, J. A. *et al.* (2005) *Science*. [2] MacArthur, R. H. & Wilson, E. O. Princeton University Press, 2001. [3] Laurance, W. F. *et al.* (2002) *Conserv. Biol.* [4] Ozanne, C. M. P. *et al.* (2003) *Science.* [5] Hutchinson, G. E. (1957) *Cold Spring Harb. Symp. Quant. Biol*. [6] Gatti, R. C. *et al.* (2017) *Plant Ecol.* [7] Klinges, D. H. *et al. Amer Nat.* in review. [8] Bergen, K. M. *et al.* (2009) *J. Geophys. Res. Biogeosciences.* [9] Basset *et al.* (2015) *PLOS One.* [10] Myers, N., *et al.* (2000) *Nature.* [11] Andreone, F. *et al.* (2008) *PLOS Biol.* [12] Böhm, M. *et al.* (2013) *Biol. Conserv.* [13] Hanse, M. *et al.* (2013) *Science.* [14] Simard, M. *et al.* (2011) *J. Geophys. Res.* [15] VanDerWal, J. *et al.* (2014). R package. [16] Lisein, J. *et al.* (2013) *Forests* [17] Webster, C. *et al.* (2018) *Remote Sens. Environ.*