A floristic, ecological and evolutionary assessment of a high rainfall savanna in mainland South East Asia: Linking functional biogeography, community composition and conservation

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Background:

Savannas are one of the world's major biomes, covering a vast environmental gradient across the wet/dry tropics of the world from 200 to 2000 mm mean annual rainfall (Lehmann et al 2011). Savanna covers over 20% of the global land surface (Bond 2008), directly supporting the livelihoods of ~ 1 billion people (Boval et al 2017). Commonly considered a poor cousin of tropical forests in terms of diversity, new research has shown that high rainfall savannas (where mean annual rainfall > 700 mm (Ratnam et al 2011)) can support a diversity of birds, reptiles and mammals equal to tropical forests (Murphy et al 2016). However, high rainfall savannas are threatened by drastic agricultural expansion that is already underway (Estes et al 2016), and forest expansion which encroaches on high rainfall savannas (Stevens et al 2016), leading to declines in biodiversity and the loss of critical ecosystem processes (Lehmann and Parr 2016).

The savanna biome is often treated as homogenous, leading to oversimplification and significant errors in our ability to predict their resilience to climate change (Lehmann et al 2014). Research has shown that savannas on different continents occupy different climatic niches and that arid savannas display different vegetation dynamics to high rainfall savannas (Lehmann et al 2011). Further, the composition of understory plants can be used to delineate ancient savannas from those derived from deforestation (Veldman 2016). That is, grouping all grasses, trees and forbs into single functional types independent of origin ignores differences in species diversity, adaptive traits, and evolutionary history, all of which have a profound impact on our understanding of the savanna biome (Moncrieff et al 2014, Lehmann et al 2014).

High rainfall savannas in South East Asia have often been misidentified as degraded forests (Ratnam et al 2011) leading to inappropriate management and a misinformed biodiversity conservation perspective. Fossil evidence suggests that the Asian savannas predate humans (Ratnam et al 2016), and past climatic evidence suggests that savannas in Southeast Asia were more extensive than they are today (Louys et al 2010). Successful conservation of extant savanna sites requires an understanding of their ecology and evolutionary history, especially since Southeast Asian savannas are severely threatened despite supporting unique floral diversity in ie tribe Andropogonae (Poaceae) (Arthan et al 2017). Asian savannas are threatened by agriculture and government driven afforestation initiatives (Ratnam et al 2016). In this context a greater understanding of ancient savannas is crucial.

Study aims:

Although I had hoped to answer questions around distinguishing derived vs natural savannas, time constraints overall resulted in this idea being reserved for future work. In the field therefore, data were collected to pursue the following aims;

1) **To establish a minimum and maximum age for high rainfall Cambodian dipterocarp savannas, and to extrapolate whether they are of anthropogenic origin or not.**

i) By using overall species composition data to identify whether there is a significant endemic element which would indicate antiquity

ii) By using *Ziziphus* Mill. as a model genus to establish the ages of high rainfall savannas.

iii) By collecting silica samples and herbarium vouchers across *Ziziphus* diversity in order to sequence the genus to assess phylogeographic structure.

iv)By investigating evolutions into and out of high rainfall savannas using *Ziziphus* as a model genus.

2) **To assess the resilience of the savanna to future structural change**

i) By collecting compositional data along a canopy light gradient

ii) By assessing functional trait changes along a light gradient

iii) By investigating whether patterns of understory species diversity change seen in South East Asia are replicated in East Africa

3) **To compare data on floristic composition and functional traits across mesic savannas in order to see whether evolutionary filtering by fire overrides biogeographic signals.**

i) By measuring and recording functional traits in Siem Pang Protected Forest and comparing these to data from African savannas in order to gain insights into the similarities and dissimilarities in community traits between intercontinental high rainfall savanna species.

ii) By collecting silica-gel dried leaf samples of forb and grass diversity for future phylogenetic analysis to assess phylogeographic community structure.

In order to undertake this, plots were established along a canopy gradient in the Western Siem Pang protected area at locations shown in Fig 1.

Field site:

Western Siem Pang, in the Stung Treng province of North Cambodia, is a designated Important Bird and Biodiversity Area, and a BirdLife Forest of Hope. It completes a network of protected areas that spans the borders between Laos, Cambodia, and Vietnam, covering 700,000ha in total. It supports globally irreplaceable local populations of Giant and White-shouldered Ibis, and three species of globally threatened-critically endangered vultures (BirdLife International Cambodia Programme, 2012). Around 70,000ha of Western Siem Pang is deciduous dipterocarp forest and grasslands which burn annually (BirdLife International Cambodia Programme, 2012).

Tropical and subtropical dry broadleaf forests have been considered synonymous with densely wooded, high rainfall savannas (Murphy, Andersen and Parr, 2016), therefore the deciduous dipterocarp forest could more accurately be described as savanna. This is reinforced by the presence of an understory of C_4 grasses, and the fire-adapted traits of the woody flora (Ratnam *et al.*, 2016). No systematic botanical work has been undertaken in Western Siem Pang, and only the vegetation of the wetlands has so far been surveyed (BirdLife International Cambodia Programme 2012). However, Murphy, Andersen and Parr (2016) found that the dry tropical forests of central Indochina were some of the most species rich for vascular plants. This study aimed to significantly increase our understanding of a plant community which has historically received little floristic attention.

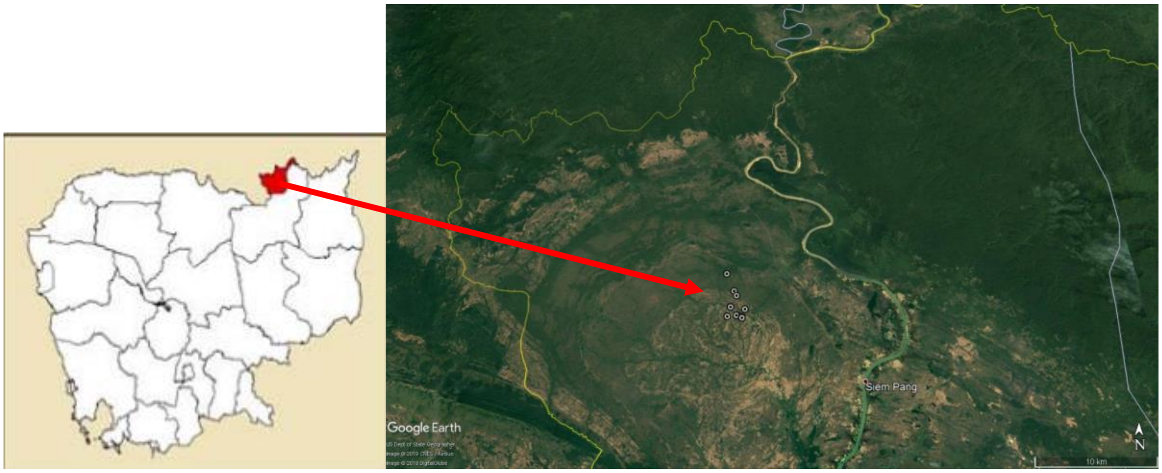

Figure 1, The Location of Western Siem Pang within Cambodia, and plot locations in the field (Google Earth Pro 2019)

How old are dry deciduous dipterocarp savanna in mainland South East Asia?

Ziziphus (Rhamnaceae) is a cosmopolitan genus with species number estimates varying from 30 (Heald 2004) to ~170 (Islam and Simmons 2006). It has a predominantly southern hemisphere distribution and could be of Gondwanan origin (Richardson et al 2000). The genus includes *Ziziphus jujuba* Mill., a plant of notable economic value for its edible fruits. Within the Ziziphoid group, genera and tribes are usually confined to a particular continent. *Ziziphus*, however, is found across Asia, Africa, North and South America, Oceania, and Europe (Richardson et al 2004). The processes leading to high rates of diversification in Rhamnaceae are continent dependent (Onstein et al 2015), therefore phylogenetic comparative methods on a globally distributed clade across multiple ecosystems could be applied to study convergence at large temporal and spatial scales (Onstein and Linder 2016). Species such as *Z. jujuba* and *Z. mauritiana* Lam. are widely distributed, whereas *Z. spina-christi* (L.)Desf has a restricted range (Arndt et al 2001). Dry adapted species include *Z. mucronata* Willd. (in Africa), and *Z. mauritiana.* While C_4 grasses are the dominant savanna vegetation, they have been shown to rapidly replace or be replaced in dominance by other grasses (Dunning et al 2017) making dating the biome using Poaceae to be problematic.

Utilising a cosmopolitan woody genus (*Ziziphus)* with some well dispersed and some restricted species should enable more effective dating of the origin of high rainfall savannas. Since savanna tree species are typically derived from local forest ancestors (Maurin et al 2014, Simon et al 2009) this should also clarify evolutionary shifts into and out of biomes. *Ziziphus* is locally dominant in Southeast Asian savannas, and in Cambodia, *Z. cambodiana* Pierre is used to treat a number of complaints including stomach ache (Chassagne et al 2016). The most comprehensive *Ziziphus* phylogeny to date undersampled Old World taxa (11 out of 150 species) and resolved *Ziziphus* as paraphyletic (Islam and Simmons 2006). None of the Old World specimens used in the Islam and Simmons study were from Cambodia or any of the neighbouring countries (Islam, M. pers. comm). By adding to existing phylogenies through extensive sampling of herbarium specimens and in situ collections, the biogeography of *Ziziphus*, and the evolution of traits such as xeric or fire adaptations can be placed and dated. Further, the taxonomy of *Ziziphus*, which is currently a little unclear, could be clarified by a whole genus approach to sampling.

I was successful in collecting *Z. mauritiana*, *Z. oenopolia*, and *Z. cambodiana* which has previously not been included in phylogenies at all (Fig 2) and one as yet unidentified species of *Ziziphus*. The collection and inclusion of these specimens may enhance our knowledge and understanding of high rainfall savanna biogeography and evolutionary history. Further, these collections will facilitate future taxonomic work, regional checklists and national flora, as well as adding to herbaria and molecular resources.

Figure 2 *Ziziphus* species collected during the trip (L-R: *Z. cambodiensis, Z. oenoplia, Z.mauritiana*)

If the deciduous dipterocarp savanna is ancient, then it is likely that it will support high levels of endemism in Poaceae (Vorontsova et al 2016). Recent work on tribe Andropogonae in Thailand identified a previously unidentified lineage and revealed a unique diversity in Southeast Asia (Arthan et al 2017). Collections, and subsequent molecular and morphological investigations of the Andropogonae in Cambodia may well reveal both unidentified lineages and cryptic species. A systematic inventory of Andropogonae in deciduous dipterocarp savanna will add to herbaria collections as well as supplement our knowledge of the taxonomy and diversity of Poaceae in Southeast Asia (Fig 3). The grass flora was sampled as described below under ‘Methods’, and levels of endemism will be compared with other continental regions.

Figure 3 Grass diversity in the field (Grasses currently being identified by Henry Noltie)

How resilient is the high rainfall savanna to future structural change?

High rainfall savannas globally are under threat (Parr *et al.* 2014, Bond 2016). Misidentification as degraded forests has left them vulnerable to afforestation projects, conversion to agriculture, and fire repression policies (Ratnam *et al*. 2011, Ratnam *et al.* 2016). Rising atmospheric CO_2 lessens the ecological advantage of the C_4 photosynthetic pathway for the grasses which define this ecosystem, and increases the risk of woody encroachment (Devine *et al.* 2017).

Encroachment fundamentally changes the ecosystem functioning of the savanna, reducing water availability (Honda and Durigan 2016), biodiversity (Smit and Prins 2015), and potentially affecting livelihoods. As the canopy closes, C_4 grasses are quickly shaded out (Charles-Dominique *et al.* 2018). These grasses are often highly flammable, and their reduction lessens the possibility of fire (Simpson *et al.* 2016). Without fire, trees are more likely to colonise the mesic savanna, leading to a biome shift (Bond, Woodward and Midgley 2005, Hoffmann *et al.* 2012).

Divergent shade tolerances between species co-occuring in a habitat is a fundamental aspect of ecosystem dynamics (Valladares *et al.,* 2016). The gradient of tree canopy cover in mesic savannas creates spatial heterogeneity by intercepting available light (Hoffmann *et al*. 2005). The shade imposed by trees acts as an environmental filter, changing community structure and composition (Abdallah *et al.* 2016). C_4 grasses which dominate the savanna ground layer are adapted to function in high light conditions (Edwards and Smith, 2010). Studies in the USA have shown negative correlations between tree cover and C_4 grass species richness (ie Veldman, Mattingly and Brudvig, 2013), however the cover of N fixing forbs positively correlates with tree cover (Peterson, Reich, and Wrage, 2007). Research into the effects of shade gradients on the savanna ecosystem has tended to focus on grass biomass or woody recruitment in low rainfall savannas (ie Vadigi and Ward 2013, Belsky 1994). Little if any attention has been paid to herbaceous species composition.

Figure 4, Examples of the canopy cover gradient (L-R: 10%, 40%, 80%)

Differences in shade tolerance are fundamental to our understanding of community ecology (Valladares *et al*. 2016). By quantifying the impact of canopy cover and light availability on grass and forb composition and diversity, I can gain a new understanding of the resilience of the high rainfall savanna ecosystem to structural changes.

Plant composition data and herbarium specimens were collected as described in 'Methods' at canopy covers of 10%, 20%, 40%, 50%, and 80% (Fig 4). Canopy cover was established using a densitometer and hemispheric photographs were taken for corroboration and later analysis. Once collections have been identified I will analyse changes of community composition and species richness along this light availiability gradient. These data will be compared to future floristic and ecological work in Africa and a second field season in Cambodia.

Do functional traits vary across high rainfall savannas or are some traits geographically constrained?

High rainfall savannas burn frequently, with a mean fire return time of 1 – 5 years (Archibald et al 2013) in contrast to arid African savannas where mammalian herbivory lowers fire frequencies or excludes fire entirely (Archibald and Hempson 2016). Fire acts as an environmental filter sorting plant communities across the globe (Archibald et al 2013). However, adaptations to fire have been shown to be relatively simple, evolutionarily labile, and to have evolved multiple times (Simon and Pennington, 2012). Functional traits drive community assembly and species diversity (Kunstler et al 2015). In strongly filtered communities interspecific functional variability is limited, and intraspecific variability plays a key role in resilience and community structure (Dantas et al 2012). Underground storage organs are present as a fire-adaptation in African and South American savannas but not in Australian savannas. They have not been reported in South and Southeast Asia, perhaps because it is an understudied area (Maurin et al 2014). Other adaptations include small, thick, tough leaves (Dantas et al 2012) and fast regeneration, although specific adaptations vary geographically (Bond and Keeley 2005). Using the collections made in Western Siem Pang I can investigate whether the ground layer of high rainfall savannas from Africa and Cambodia share adaptive suites of plant traits related to fire. Studies in the Brazilian Cerrado have found greater intraspecific variability within fire communities (ie locally) than between communities (ie regionally) (Dantas et al 2012). Using the collected functional trait data from Siem Pang Protected Forest I will investigate whether the pattern identified between and within fire communities in Brazil is repeated in Cambodia, and in comparing these data with data from Africa, whether phenotypic traits in plant communities filtered by fire are constrained by geography or whether intraspecific variability on a global scale varies more regionally than locally.

Collections were made of 381 specimens, with one set deposited in the herbarium of the Royal University of Phnom Penh and the second set brought back the herbarium at RBGE. Although full identification is still in progress, specimens were collected from 45 families.

Methods:

Plot data was collected following Vorontsova *et al.,* (2016). Areas dominated by deciduous dipterocarp tree genera were identified, and a 50m plot laid out. At the centre of each plot, hemispheric canopy photos were taken for later calculation of Leaf Area Index (LAI) and GPS recorded. A densiometer was used to categorise the percentage cover from trees. A gradient of canopy cover was established from 10%-80% with two plots at each level of 10%, 20%, 40%, 50%, and 80%.

Four transects 25 m each were placed in a radial pattern from the centre plot at N, S, E, and W (Figure 5). A circle 1m diameter was placed at 5m intervals along each transect. When a transect was judged to cross into a different vegetation type it was terminated before the transition to ensure a single site represented a single community. All herbaceous species in the circle were recorded and herbarium specimens made for each species. These were deposited in the Royal University of Phnom Penh and RBGE herbaria. These specimens are being used for identification and clarification of species, and identifying traits. Traits identified in the field were broad functional groupings, and traits which have yet to be identified include plant architecture and storage organs.

Since soil is likely to be a factor in species diversity, sites were placed in areas of homogenous underlying geology, and soil samples were collected from each site. Soil samples of the surface 10cm were taken at the corner and centre plots as shown in Figure 5. Samples from each site were bulked and dried and 200g brought back to Edinburgh for analysis. Analyses will include total soil N and pH.

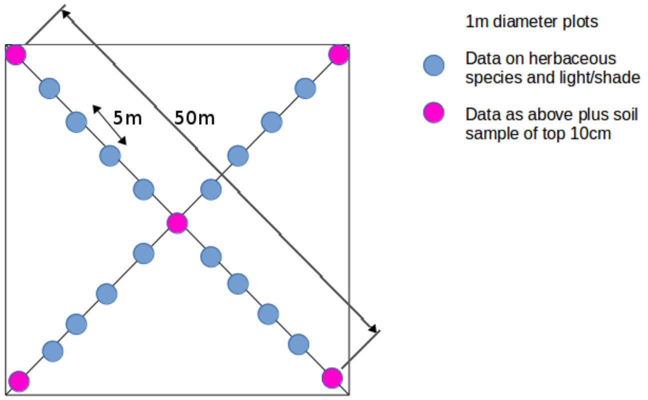

Figure 5, Plot method for full capture of understory species diversity. Modified from Vorontsova et al (2016).

Project outcomes:

This research forms part of my Ph.D. dissertation, however more work is required before the results can be published. Outputs so far include

1. Herbarium specimens of high rainfall savanna grass and forb species deposited in RBGE and Royal University Phnom Penh (RUPP) herbaria (currently being identified).
2. Silica-gel dried leaf samples for future evolutionary genetic investigations of Poaceae tribe Andropogonae.
3. I am working towards a more complete *Ziziphus* phylogeny including 4 species specifically collected from Cambodia added to existing phylogenies which can facilitate taxonomic revision.
4. Links with BirdLife International and collaborative ties with conservationists in Southeast Asia.
5. An updated checklist of plant species of Western Siem Pang for the BirdLife biodiversity team (in progress).
6. Future presentations will include a Science Research Club at RBGE and a conference presentation in the academic year 2019-2020.

Schedule:

Date	Activity
November 1	Fly to Phnom Penh
November 2-3	Meetings with colleagues at RUPP herbarium
November 4	Fly to Siem Reap
November 5-6	Planning
November 6-27	Field work in Siem Pang
November 28-29	Sort specimens
November 30	Fly to Phnom Penh and deposit duplicates at herbarium
December 1-15	Self-funded travel
December 16	Return to Edinburgh

Expenditure:

Return flight to Phnom Penh -Jess	£723.36
Return flight to Phnom Penh - Hazel	£766.66
Travel within Cambodia	£100.91
Accommodation	£167
Food	£115
Driver hire	£158
Driver food and fuel	£235
Specimen postage	£175
Visas	£46
Vaccinations - Hazel	£213
Vaccinations - Jess	£247
Newspaper for pressing	£7.53
Total	£2954.46
Awarded from Davis Expedition Fund	£3200
Total remaining	£245.54

The remaining £245.54 will be put towards a second field season in Cambodia.

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