REVIEW ARTICLE

Dead wood fungi in North America: an insight into research and conservation potential

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Abstract

Saproxylic fungi act as keystone species in forest ecosystems because they colonise and decompose dead wood, facilitating colonisation by later species. Here, we review the importance of intact forest ecosystems to dead wood fungi, as well as trends in their diversity research and challenges in conservation. Saproxylic communities are sensitive to transition from virgin forests to managed ecosystems, since the latter often results in reduced tree diversity and the removal of their natural habitat dead wood. The impact of dead wood management can be quite significant since many saproxylic fungi are host-specific. The significance of citizen science and educational programmes for saproxylic mycology is discussed with the emphasis on the North American region. We intend to raise the awareness of the role that dead wood fungi play in forest health in order to support development of corresponding conservational programmes.

Keywords

Introduction

Dead wood is an essential component of any forest ecosystem. Its value for biodiversity and forest ecosystem function is hard to underestimate; dead wood protects soil against erosion, contributes to soil quality with massive organic and mineral inputs, improves water retention and creates multiple habitats for plants, animals and fungi (Stokland et al. 2012). Components of dead and decaying wood provide the energy necessary to

facilitate the regeneration of trees in the form of carbon and nitrogen storages. In undisturbed and old-growth forests, dead wood exists in many forms, from entire standing or fallen trees to decomposing fragments of wood. These diverse woody elements co-exist across time and space. Dead wood is a challenging substrate to decompose. Enzymatic digestion of tough woody polymers such as lignin and cellulose is primarily performed by saproxylic fungi and bacteria, whose actions are complemented with additional mechanical disintegration by invertebrates (Keren and Diaci 2018). Saproxylic fungi thrive in temperate (Hodge and Peterken 1998; Purahong et al. 2018), as well as in other types of forest, facilitating cycling of nitrogen and other elements back to forest soils (Juutilainen et al. 2016). In addition, as pioneer decomposers, saproxylic fungi initialise ecological succession processes that sustains forest biodiversity, which makes them invaluable forest organisms. Numerous dead wood fungal species have been described with more being discovered regularly, but the knowledge about their diversity or species loss remains scarce (Hawksworth 1991; Runnel and Lohmus 2017). Importantly, some saproxylic fungal species have specific preferences for substrate types, such as coarse woody debris (CWD) or standing dry trees (Nordén et al. 2013).

Earlier research demonstrated that in North American forests, decomposing CWD could cover up to 25% of forest ground surface (Speight 1989), with dead wood making up a third of total woody biomass in most ancient forests. In a managed North American forest, dead wood content can be reduced by up to 15% from its original amount (Harmon 2001). This reduced proportion is a result of a combination of factors such as land management practices, forest type and climate change. Forests, especially in the circumboreal zone, are experiencing some of the largest global warming-induced temperature increases on earth, resulting in yearly tree loss due to increased exposure to insect infestations as well as more frequent wildfires (Balling et al. 1998; Hansen et al. 1996; Serreze et al. 2000; Soja et al. 2007).

To sustain human activity, forests continue to be cleared and the land is transformed to suit the immediate need (DeFries et al. 2004; Vitousek et al. 1986). Older trees are regularly removed for timber or to make room for agriculture or urban sprawl. However, as population needs and infrastructures evolve, unused croplands may transition back to forests. Nevertheless, most replanted forests are far too young (Tierney et al. 2017) and they lack the structural complexity needed to support diverse saproxylic organisms. In highly populated regions, any decomposing wood that could potentially accumulate is periodically removed for fuel, decorative purposes or when 'cleaning' the landscape (Fig. 1) (DeFries et al. 2004). In addition, logging is a common strategy in forest management to guard against the spread of species targeting decomposing wood (Karvemo et al. 2017). For example, bark beetles are natural inhabitants of old-growth trees and their control has started a debate between loggers and environmentalists who disagree on the best way to combat them (Grotta 2013; Stokstad 2017). Similar controversy dominates the discussion of use of controlled/prescribed burning for dead wood restoration (Eales et al. 2016).

The aforementioned factors have led to habitat loss and a sharp decline in species diversity amongst various taxa of all saproxylic organisms and especially fungi (Jonsson et al. 2005). The removal of dead wood has resulted in an incalculable extinction

Figure 1. Managed park with almost no dead wood. New Jersey, USA, 2018. Photo M. Shumskaya.

debt facing saproxylic taxa worldwide (Chen and Hui 2009; Hanski 2000). For example, out of 45 well studied saproxylic beetle species existing during the Bronze Age, less than 1/3 have avoided extinction and were considered rare 30 years ago (Speight 1989). The reduction in dead wood habitat lowers saproxylic species richness and decreases genetic diversity within populations, leading to rippling consequences for forest ecosystems specially adapted to vast saproxylic communities and leaving them vulnerable to disturbances and extinction (Sebek et al. 2013).

Most of ongoing conservational efforts aim to restore falling biodiversity of plants and animals via assigning spaces and/or species official designations, like endangered or threatened, accompanied by legal protection (Juutilainen et al. 2016). Unfortunately, logging of damaged or dead trees (salvage logging) in both North America and Europe is often conducted even in areas reserved for conservation and otherwise protected from logging, decreasing the biodiversity of saproxylic species (Thorn et al. 2018). Current forest management and conservation strategies are not sufficient to preserve saproxylic biodiversity, in particular fungi that are specialised to CWD (Abrego and Salcedo 2013; Küffer and Senn-Irlet 2005). Little is being done to protect saproxylic biodiversity in the face of habitat loss and other anthropogenic threats. However, there are recent initiatives of the IUCN (International Union for Conservation of Nature) such as the Global Fungal Red List Initiative (http://iucn.ekoo.se/iucn/about) or European Red List of Saproxylic Beetles (Nieto and Alexander 2010).

In this work, we intend to overview the current knowledge on the dead wood fungi biology, ongoing research and conservation with the emphasis on North America to promote public education, research and conservation programmes in saproxylic mycology in this region.

Dead wood fungi at a glance

Saproxylic fungal communities constantly transform as wood decomposes. The decomposition pathways vary greatly amongst the tree species, surrounding biotopes, the landscape matrix, forest history, spore rain and numerous other factors. This process depends highly upon the structure and composition of the saproxylic fungal community (Kubartová et al. 2015; van der Wal et al. 2015). Different types of saproxylic fungi demonstrate a gradient of enzymatic abilities and, traditionally, are classified according to the specific substrates they digest and the type of resulting rot. In general, white rot refers to fungi that can process lignin, brown rot fungi digest hemicellulose and soft rot fungi possess enzymes that break down cellulose (Rajala et al. 2015). As Boddy and collaborators (Boddy et al. 2007) demonstrated, wood-decaying fungi latently colonise living angiosperms and, after the trees are dead or damaged and water content in the sapwood is reduced, the fungi start to form fruit bodies.

Once started, decomposition gradually accelerates. Initially, when the wood is still very rigid, the heartwood is dominated by white-rot fungi; as fungi reproduce and develop, the number of brown-rot species increase heavily (Fig. 2) and the decomposition reaches its intermediate stage (Hiscox and Boddy 2017; Mäkinen et al. 2006) with fungi forming fruit bodies from early to late decay stages (Fig. 3). Finally, when wood is nearly completely broken down, the fungal fruiting bodies are no longer visible (Renvall 1995).

Figure 2. Brown rot of *Fomitopsis pinicola*, a common polypore on European spruce, *Picea abies*. Finland, Sipoo, Rörstrand, 2013. Photo D. Schigel.

Figure 3. Fungal fruit bodies are formed as wood decomposes and fungal species compete for resources and succeed each other. Bright annual fruit bodies of *Laetiporus sulphureus* on oak logs. Lithuania, Punios šilas, 2017. Photo D. Schigel.

Fungal hyphae absorb nutrients from degraded wood, then grow and expand until they reach and intertwine or penetrate roots from surrounding trees and plants. Mutualistic relationships between fungi and plants allow plant roots to use much of the absorbed minerals (Baldrian 2017), greatly expanding the surface area and absorption capabilities of the root system. In return, trees and plants provide heterotrophic fungi with carbohydrates and sugar (Bobiec et al. 2005). This absorption system, while sophisticated, is not 100% efficient, leaving excess nutrients to pool in the soil and mineralise, encouraging seedling recruitment. Nearly all the nutrients held in densely shaded soil are provided and replenished by fungal hyphae. Fungal mycelium also lends structural support to soil which slows the rate of erosion (Zhang et al. 2016). Few people, outside of specialised researchers, realise the link between the dead wood, soil quality and soil stability; without the continuous presence of saproxylic fungi and dead wood, soil quality diminishes (Hartmann et al. 2012), producing low quality vegetation as land becomes unsuitable to sustain seed recruitment and development.

Research on saproxylic fungi: challenges

Alternating life cycles and reproduction patterns of fungi render quantifying and collecting samples a challenging task as the detectability of different species greatly varies

within and across fungal taxa, with many species being cryptic (Halme and Kotiaho 2012; O'Brien et al. 2005). In order to get an inclusive picture of the local saproxylic fungal community, study sites must include all present tree species, need to be sampled repetitively, across a large spatial scale and over more than one growing season since fungal communities vary between decomposition stages which can continue through multiple decades (Saint-Germain et al. 2007). Until recently, few well-designed studies on saproxylic fungi were completed on a scale large enough to overcome these obstacles. Most of the research was being done on CWD (Grove and Forster 2011), with smaller diameter dead wood largely neglected in favour of larger samples housing more saproxylic organisms (Juutilainen et al. 2011) with some exceptions (Juutilainen et al. 2014). Regionally, studies of boreal forests overwhelmingly dominate in traditional dead wood conservation (Seibold et al. 2015), while tropical and subtropical forests, the greatest biodiversity hotspots on earth, remain vastly understudied (Dirzo and Raven 2003; Hansen et al. 2008).

Fortunately, the recent introduction of new sampling and molecular sequencing techniques and metagenomics (metabarcoding) as well as development of worldwide online DNA databases has greatly improved the research of cryptic dead wood fungal communities (Taylor et al. 2014). Metagenomics (metabarcoding) works with all of the genetic material from an environmental sample then analysing DNA sequences for all of the microorganisms present, using next-generation sequencing (NGS) techniques (Otlewska et al. 2014). The resulting sequences are compared against the reference libraries of Sanger sequences of well-identified specimens and thus multispecific metabarcoding samples are identified. This method allows collecting wood debris as samples in addition to fungal fruiting bodies to discover all cryptic or hidden species. Fruit body surveys combined with metabarcoding provide accurate, comprehensive data on saproxylic ecology (Ovaskainen et al. 2013).

With the use of molecular methods, we finally can start to understand the details of the dynamics of wood decomposition and the assembly processes of saproxylic fungi (Stokland et al. 2012). We now know that fungal micro-ecosystems are far more complex than once thought. Not only are there far more species of saproxylic fungi in existence than we thought, but the dynamics of succession and species assembly associated with dead wood decomposition are variable and adaptable and continues in the soil (Mäkipää et al. 2017). Researchers have even observed a pronounced preference for different tree species amongst saproxylic fungi that is comparable to, if not greater than, that of symbiotic and parasitic fungal taxa (Purahong et al. 2018). Metagenomics allows large-scale studies to be performed on dead wood to produce global data on saproxylic fungal biodiversity, essential to devise a working conservation strategy (Baldrian 2017; Telfer et al. 2015).

The use of DNA techniques in saproxylic ecology makes it an intriguing, complicated, multi-factor interdisciplinary field that incorporates the most current technologies. In spite of the global importance of dead wood, currently nearly all publications on saproxylic mycology come from Nordic countries and Canada, where forest research benefits from studies on complex interactions between fungi and other organ-

isms (Heilmann-Clausen et al. 2017; Mäkinen et al. 2006); dead wood as a study system is less popular in the United States.

A possible explanation for this imbalance in research reports is an enculturated social prejudice toward fungi. In the United States of America, fewer undergraduate students majoring in biology are choosing fundamental research careers, especially in mycology, when juxtaposed with more glamorous options like health and business professions (Sauermann and Roach 2012). The fact that so little is known about the importance and functionality of fungi exacerbates the problem and perpetuates the cycle. Fungi are often considered as pesky landscape invaders, or something purchased at the local supermarket instead of vital members of a global ecosystem. If more undergraduate students and the general public understood the central role played by saproxylic fungi in nutrient cycling processes of the world's largest carbon stores and the subtle beauty of saproxylic organisms, their research would likely garner more attention. The Nordic, British and Japanese admiration for dead wood and saproxylic organisms is yet to find its way into the North American academic tradition.

Research on saproxylic fungi: can citizen science help?

Citizen science is a research performed by laymen guided by a research professional. It has been shown to effectively support biodiversity and conservation studies (McKinley et al. 2017), hence research in biodiversity of fungi (saproxylic in particular) can especially benefit from involvement of citizen scientists. There is an ongoing effort across the mycology community to collect and organise data on all new and existing fungal species, whose number is estimated to be around 3 million (Funk et al. 2017; Hawksworth 1991; O'Brien et al. 2005; Tedersoo et al. 2014). Currently, not only research universities, but also undergraduate colleges as well as citizen scientists across the globe participate in this project. "Amateur scientists" collect observations, photographs and tissue samples for DNA analysis in an effort to establish an extensive and accurate database and participation in research becomes more and more popular in the US. Numerous informal interest groups and citizen science initiatives have sprouted on the Internet (North American Mycoflora www.mycoflora.org, Mushroom Observer http://mushroomobserver.org, Denmark's Mushroom Atlas http://www.svampeatlas. dk, https://svampe.databasen.org, Finnish Atlas of Fungi http://sieniatlas.fi and many others). Citizen science data is aggregated together with professionally collected data by thematic and national biodiversity portals; the central access point and search is provided by the Global Biodiversity Information Facility (GBIF). By October 2018, over 80% of the world's digital biodiversity data in GBIF have been comprised by human observation records (www.gbif.org).

Active development of citizen science in saproxylic mycology would not only contribute to fundamental research, but also help to raise the awareness on the role of dead wood and its inhabitants to support conservational efforts. While mushroom hunters commonly collect macrofungi, educational programmes can help to direct their at-

tention to dead wood species and research centres can support DNA-barcoding of the collected cryptic samples. A collaborative project on macrofungi, the North American Mycoflora, has already started in the US in 2017 to facilitate collaboration between professional mycologists and citizen scientists.

Saproxylic fungi conservation

In general, there is a limited conservation effort to address overall fungal biodiversity, especially when compared to other taxa; the Red List of threatened species from the International Union for Conservation of Nature includes only 56 threatened Fungi, while listing 68,054 Animalia and 25,452 Plantae. The Endangered Species Act in the United States of America is not any different, listing only 2 Fungi (lichens), while including 1,459 Animalia and 947 Plantae. Most of the countries in the world lack national Red Lists of fungi (Willis 2018). The low number of fungi on the Red Lists can be partially explained by a perception of many scientists that fungal species are problematic to assess due to their cryptic nature, high diversity and lack of taxonomic, distribution and ecological data (Mueller 2017). Insufficient representation of fungi in the IUCN lists limits conservation efforts, which are currently inadequately low to preserve the known biodiversity of 120,000 fungal species, with the various worldwide estimates of 1.5–3.8 million species (Blackwell 2011; Hawksworth 1991, 2001; Hawksworth and Luecking 2017; Tedersoo et al. 2014). The highest number of fungi was described in 2017 in Asia (35%), far ahead of North America (9.5%), reflecting the imbalance of taxonomic effort (Willis 2018). Since less than 8% of species are believed to have been identified (Hawksworth and Luecking 2017; Mueller and Schmit 2007) and more than 1,000 species are being described each year (Hawksworth 2001), it is imperative to evaluate techniques to assess the conservation status and protect fungi and specifically saproxylic fungi, their habitat and their associated species.

A common strategy to combat biodiversity loss due to urban development is setting aside areas of forested or re-forested land specifically to serve as nature and wildlife conservatories (Suominen et al. 2015). Saproxylic species, however, cannot be effectively protected using re-forestation methods. In re-forested areas, trees often lack diversity and are typically young, so they will not begin to decay in the near future, breaking the temporal continuum of dead wood for saproxylic organisms to inhabit. Even if decomposing wood still somehow manages to accumulate, current land management practices typically call for removal of woody debris and thus remain saproxylic biodiversity unfriendly. As human populations remove or alter forests, saproxylic fungal populations decline (Abrego et al. 2014; Caughley 1994; Komonen and Muller 2018; Mäkipää et al. 2017; Ovaskainen et al. 2017). Decreased tree diversity and corresponding dead wood leads to an unavoidable decline in saproxylic fungal diversity (Purahong et al. 2018), which would impact other species that

depend on fungi to soften dead wood before it can be inhabited. Setting aside truly unmanaged, untouched forested areas will help to preserve saproxylic diversity because the overwhelming majority of dead wood fungi are habitat and species specific (Bader et al. 1995).

Saproxylic fungi in unpopulated regions such as boreal and tropical forests are not commonly exposed to the same hazards stemming from development. However, they are not exempt from serious threats to their habitat such as climate change, pollution, agricultural chemical runoff and forestry practices. As species richness decreases latitudinally from tropical regions to arctic boreal regions, diversity of saproxylic fungi is affected correspondingly, with exceptions in ectomycorrhizal and ascomycete fungi (Juutilainen et al. 2016; Luo et al. 2014; Tedersoo et al. 2014).

The good news is that, with the recent innovations in fungal research and recognition of the vital role of fungi in ecosystems, the discipline of conservation mycology is able to emerge (May et al. 2018). In Chile, for example, an impressive promotional effort of The Fungi Foundation (Fundación Fungi) has led to the inclusion of fungi into Chile's General Environmental Framework Law in 2010 requiring a mandatory inventory of fungal species, with an obligation to develop fungal baseline studies established in 2013 (www.ffungi.org). As a result, Chilean fungi are now considered when evaluating projects that alter natural environments of Chile. In Australia, conservation mycology is strongly supported by citizen science initiatives in mapping and monitoring fungi (Irga et al. 2018). Dead wood, the habitat of saproxylic fungi, is an important subject of ecological and conservation biology research in Europe: The V European Congress of Conservation Biology in 2018 (https://conbio.org/mini-sites/eccb2018) had multiple discussions on dead wood conservation.

Support of the same magnitude can be expected in North America. A common social perception of fungi as "bad" and dead wood as an "unattractive" fire hazard that attracts pests and potentially deadly pathogens (Pastorella et al. 2016) can be improved with the proper educational programmes. Hopefully, as we start to better communicate the importance of fungi, dead wood and, specifically, saproxylic fungi to future scientists, public, broader conservation community, land managers and policy-makers, they will start to appreciate the complexity of a forest, a system much more intricate than several trees growing together in a park. Understanding of all fungi will ensure their significant inclusion in conservation actions and funding in the USA (Allen and Lendemer 2015). As of now, there is no chapter on saproxylic biology in a common school textbook, but education can be achieved through additional after-school programmes, amateur clubs for public, professional development for forest managers or special topic courses at colleges. As untouched, primeval forests (Fig. 4) are increasingly replaced by novel ecosystems, parks and reforested sites, these artificially maintained locations are quickly becoming the only places where humans interact with natural environment. The charm of the dead wood microhabitat can come through learning of the biodiversity value of the concealed worlds of hollow trees and decaying logs once they are left in parks by educated management (Fig. 5).

Figure 4. Fallen and standing dead wood are natural to primeval taiga. Russia, Altay, Balykcha, 2017. Photo D. Schigel.

Figure 5. Wild and powerful beauty of undisturbed dead wood in a protected mixed forest. Lithuania, Punios šilas, 2017. Photo D. Schigel.

Conclusions

Saproxylic fungi play a vital role in forest ecosystems. Anthropogenic pressures like climate change, pollution, urban sprawl and agricultural runoff threaten the world's forest biomes, causing dramatic loss of habitat and resulting in rapid decline of biodiversity, including the nearly invisible biodiversity in dead wood. A decline in the global population of saproxylic fungi will have cascading and far-reaching negative consequences. It is vital to raise social awareness on saproxylic organisms and incorporating saproxylic fungi into ongoing and future restoration/conservation plans, especially in North America. Educational programmes should improve the overall attitude to dead wood as an essential forest component for both park management practices and public opinion. Changing the way society views dead wood and its fungi is an important step in attracting efforts to research and conservation of saproxylic biodiversity.

Acknowledgements

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SHORT COMMUNICATION

First photographic record of marbled cat *Pardofelis marmorata* Martin, 1837 (Mammalia, Carnivora, Felidae) in Nepal

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Abstract

The marbled cat *Pardofelis marmorata* is a Near Threatened small felid. The cat's presence in Nepal is based on an anecdote. A camera trap-based study to access diversity and abundance of terrestrial mammals in eastern Nepal accumulated 3,014 camera trap days and resulted in 5,176 photographs of 17 medium-large sized mammal species. Amongst them, a marbled cat was captured at a single camera trap station in January 2018. The camera trap-capturing the marbled cat was located in the secondary forest at an altitude of 2,750 m a.s.l., dominated by free-ranging cattle close to a permanent human settlement (1.4 km) and a temporary cattle herding camp (0.4 km). This is the first photographic evidence of a marbled cat in Nepal. In this survey, we also recorded three other felid species: common leopard *Panthera pardus*, Asiatic golden-cat *Catopuma temminckii* and leopard cat *Prionailurus bengalensis*. We recommend detailed year-round camera trap surveys in the mid-hills of eastern Nepal along with research on adaptation of the small

felids to human-dominated areas and assessment of immediate threats for preparing sound conservation management plans of the marbled cat and its sympatric species. Initiation of conservation programmes engaging local *dokpa* (herders) is necessary.

Introduction

The marbled cat, *Pardofelis marmorata* Martin, 1837, is categorised as 'Near Threatened' in the IUCN Red List of Threatened Species (Ross et al. 2016) and nationally data deficient in Nepal (Amin et al. 2018; Jnawali et al. 2011). The marbled cat, listed in CITES Appendix I is a member of the Felidae family along with 14 genera and 42 species of cats (ITIS 2018). This small wild cat is a member of the bay cat lineage along with the Asiatic golden cat *Catopuma temminckii* and bay cat *Catopuma badia*. The marbled cat is similar in colouring to the clouded leopard *Neofelis nebulosa,* with dark blotches, stripes and spots. An arboreal cat with great climbing skills (Mohamed et al. 2009; Sunquist and Sunquist 2017), it is little studied (Sanderson and Watson 2011; Sunquist and Sunquist 2014). The marbled cat is slightly larger and more slender than a domestic cat (Blanford 1888–1891), with a long and bushy tail that is similar in length to the cat's body. Their sides and back are prominently smudged with irregular, large and dark-fringed markings. Black dots are embellished on legs and underparts and the tail has proximal black spots and distal rings (Sunquist and Sunquist 2017). Out of the two distinct subspecies of marbled cats, *Pardofelis marmorata marmorata* and *Pardofelis marmorata charltonii* (ITIS 2018; Kitchener et al. 2017), the latter is distributed from the foothills of Nepal, through Sikkim, Assam and into upper Myanmar (Pocock 1939). *Pardofelis marmorata charltonii* has a much thicker and longer coat than *P. m. marmorata*, with a rich ochrous-brown colour (Pocock 1939).

The forest-dependent marbled cat is distributed throughout Southeast Asia, from the Himalayan foothills of India and Bhutan to China and then southwards through to Malaysia and Indonesia. The marbled cat has been recorded in Bangladesh (Hance 2016; Khan 2015), Bhutan (Tempa et al. 2013), Brunei Darussalam (Ross et al. 2016), Cambodia (Gray et al. 2014), China (KFBG 2015; Wang and Wang 1986), India (Choudhury 1996), Indonesia (Cheyne and Macdonald 2010), Lao People's Democratic Republic (Johnson et al. 2009), Malaysia (Azlan and Sharma 2006), Myanmar (Zaw et al. 2014), Thailand (Grassman et al. 2005) and Vietnam (Nowell and Jackson 1996). Although Nepal is noted as the westernmost end of the range in distribution for the marbled cat by the IUCN Red List (Ross et al. 2016), there has been no record of direct sighting or photographic proof of the species in Nepal (Dahal and Dahal 2017).

The distribution map for the marbled cat in Nowell and Jackson (1996) shows Nepal's Nawalpur, west of Chitwan National Park, as the westernmost record of the species based on a single dead specimen record of the species (Ross et al. 2016). However, the species was not recorded inside the park at that time. The nearest confirmed record

to Nepal is from Khangchengdzonga Biosphere Reserve in Sikkim, India and further south in the Manas National Park, in Assam, India. Despite many extensive camera-trapping surveys in Chitwan National Park and other parts of Nepal, there have been no records of the live marbled cat (Dahal and Dahal 2017; Lamichhane et al. 2014; Lamichhane et al. 2016; Yadav et al. 2018). One skin of the species was collected by B. H. Hodgson and presented to the British Museum and labelled as 'Nepal' (Pocock 1939). It is assumed that the skin might have been collected during his studies between 1823 and 1843. Blanford (1888–1891) reported the marbled cat as present in Sikkim but not in Nepal. Similarly, a mammal survey report in Nepal by the Bombay Natural History Society found no evidence of the marbled cat in Nepal and speculated that Sikkim may have been the origin of the Hodgson's specimen (Hinton and Fry 1923). Pocock (1939) declared the claim of Blanford (1888–1891) to be wrong without presenting any reasons. Horsfield (1856) only mentioned 'hilly region' not the area as the habitat of marbled cat in his catalogue of the collection of Mammalia from Nepal, Sikkim and Tibet. Pocock (1939) also mentioned that the species was very hard to obtain for collection and seldom received alive by zoos. At that time, the team members of the Bombay Mammal Survey were not able to capture or buy a single animal from the indigenous people in Nepal, Sikkim, Assam and Myanmar. This also indicates the naturally potential rarity of the cat at that time.

The species is primarily found in moist and mixed deciduous-evergreen tropical forest and prefers hilly forests (Duckworth et al. 1999; Grassman et al. 2005; Holden 2001; Nowell and Jackson 1996). The marbled cat is also found in secondary and logged forests, clearings, mangroves and on the periphery of the oil palm plantations (Bernard et al. 2013; Hearn et al. 2016; Ross et al. 2010). The marbled cat's diet likely consists of squirrels and rats and birds, up to the size of pheasants (Nowell and Jackson 1996; Pocock 1932). This matches what is known from an individual in captivity (Sunquist and Sunquist 2017). Additionally, there is a report of the hunting of a juvenile male Phayre's leaf monkey by a marbled cat in Thailand (Borries et al. 2014).

The species occurs in isolated and fragmented habitat patches in some part of their distribution range (Ross et al. 2016). The loss of the habitat caused by deforestation is considered as a major threat for the species. Indiscriminate snaring is also common throughout much of its range and is likely a threat to the species (Ross et al. 2016). Body parts of this species were also reported from an illegal market of Yunan, China (Haibin and Kunming 1999). The marbled cat is also hunted for meat (Selvan et al. 2013a) and for socio-cultural rituals by some tribal groups in India (Selvan et al. 2013b). Amongst the numerous confiscations of leopard pelts, there is no record of marbled cat pelts in Nepal (CIB 2018).

Camera traps have been recording and providing new information on distribution and aspects of ecology, in recent times, of small and medium-sized wild felids throughout Southeast Asia, such as the marbled cat (Tempa et al. 2013; Thinley et al. 2015; Wibisono and McCarthy 2010). Camera traps provide absolute evidence that a species is present in an area but are not sufficient to propose conservation action without associating natural densities, habitat quality, quantity, connectivity, land use, hunting pressure etc.

The first ever camera trap photograph of a marbled cat was captured during daylight hours in Huai Kha Khaeng Wildlife Sanctuary in Thailand in 1994 (K. Conforti. pers. comm. as cited in Nowell and Jackson 1996). Similarly, the first photograph of a marbled cat in the wild was taken in Khao Yai Wildlife Sanctuary, Thailand in 1993 (Jackson 1997).

Some areas of Panchthar district (Nepal) are also connected to the protected areas of Sikkim (India) and the habitat area is similar to the habitat in Sikkim, where the occurrence of marbled cat was reported by Balnford (1888–1891). The habitat area in Nepal has much pressure from the anthropogenic activities like free-range cattle grazing, fuel wood and fodder collection.

Methodology

A camera-trapping study was conducted in non-protected forest areas of the Kangchenjunga landscape, bordering India on the eastern side, connecting the Singhalila National Park, Barsey Rhododendron Sanctuary and Khangchendzonga Biosphere Reserve, in far eastern Nepal (26°59'6.159"–27°25'57.969" N and 87°51'24.084"–88°6'34.282" E) (Figure 1). The elevation range of the study area lies between 2,000 to 4,355 m above sea level (m a.s.l.), covering about 520 km². The study area has been proposed as a conservation corridor to connect Nepal's Kangchenjunga Conservation Area (KCA) to these Indian conservation areas (Chettri et al. 2007). Monsoonal rain decreases from the beginning of October and the colder days increase in frequency, with the leaves of the deciduous hardwoods starting to fall by the end of November. This study area has been identified as a last remaining tract of Eastern Himalayan broadleaf forest, a major habitat for the endangered red panda (Williams 2003).

Dominant forest species and the composition of forest species changes with elevation, for instance *Quercus* sp. in lower temperate forest (1700–2400 m a.s.l.), *Quercus* sp., *Rhododendron* sp., and *Acer* sp*., Pinus* sp. in upper temperate forest (2400–2800 m a.s.l.), *Rhododendron* sp., *Betula* sp. and *Acer* sp. in subalpine forest (around 3000 m a.s.l.) and shrubby rhododendron species and junipers in the alpine zone (Dombremez 1976, as cited in Jackson 1994). Free range grazing has been in practice in the region for more than 170 years (Hooker 1889), is prevalent above 2,500 m a.s.l., impacting the forest area with over-grazing and has been listed as a major threat for biodiversity conservation (Shrestha et al. 2008).

A camera trap study was conducted to inventory the medium- to large-sized mammalian fauna in the region between December 2017 and June 2018, encompassing two seasons; winter (December 2017–February 2018) and spring (March-June 2018). The whole study area (Figure 1) was considered as a single block. The area above 2,000 m altitude was first selected by geoprocessing in ArcGIS 10.2. Then, we imposed uniform grid cells of 2 km × 2 km throughout the selected area. This resulted in 211 grids, of which 60 grids were sampled based on habitat type and accessibility. During field sampling, we omitted private forest areas and difficult rocky mountain
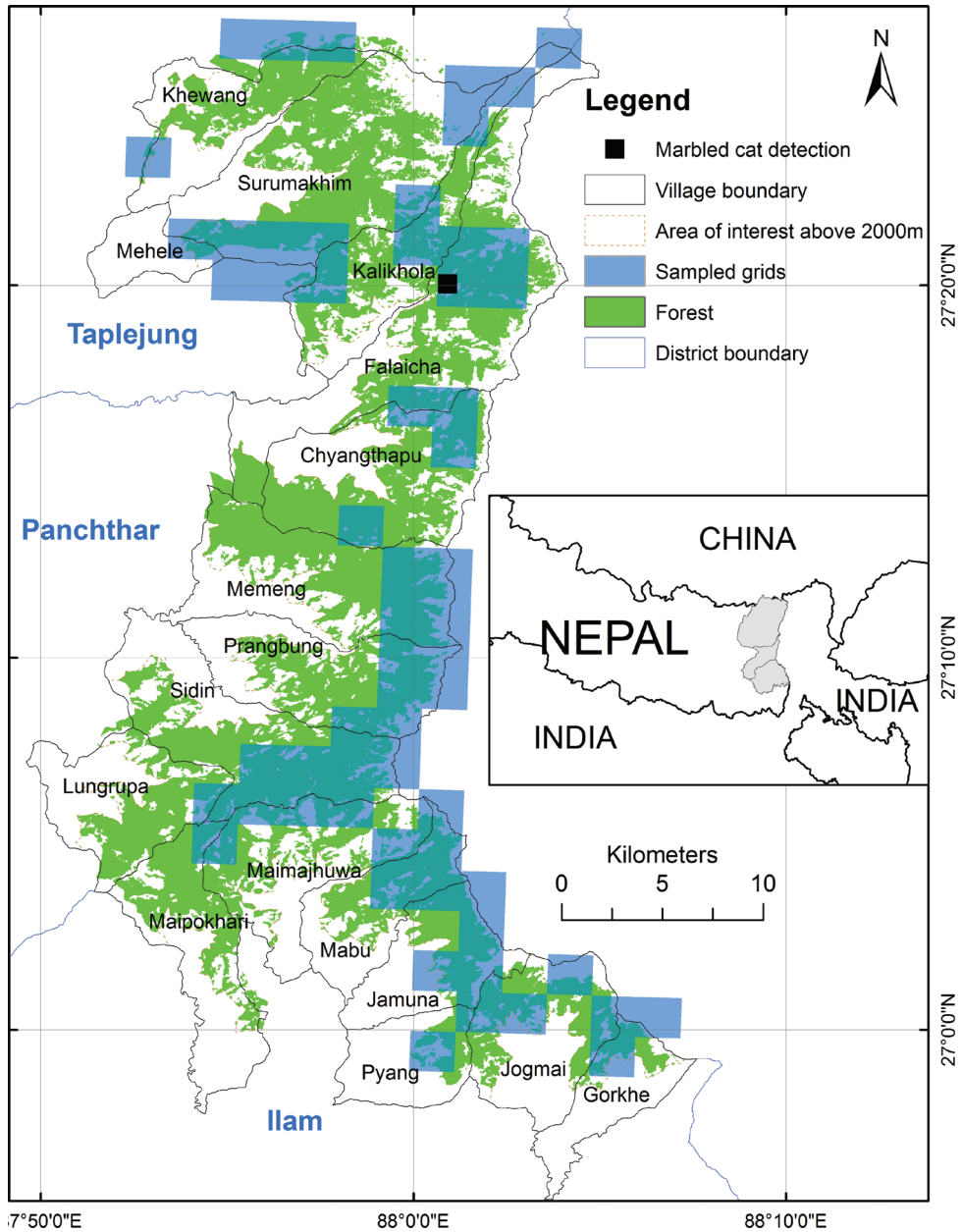
Figure 1. A map of the study area in Southern Kangchenjunga Landscape in eastern Nepal showing sampled grids in blue and location of the marbled cat detection.

cliffs and steep-mountain slopes because of inaccessibility. Within a selected grid, active trails and major areas of interest to wildlife, containing water sources, denning areas, major passes along mountain ridges and mineral licks, were chosen for the installation site of the camera traps.

We used 63 passive infrared camera trap units (51 Bushnell TROPHY Cam HD camera trap units from Bushnell Outdoor Products, USA and 12 units of Strike Force Elite camera traps, Model BTC-5HDE from Browning, Australia). The location and altitude of each site were recorded using a Garmin eTrex 10 and Rino120 handheld GPS.

On average, the cameras were left in the forests for 28 trap days. The minimum trap days for a camera was 14 days while 78 days was the maximum. The camera traps were installed at 107 locations. Cameras were secured to available tree trunks. The sensor height of the cameras installed above ground level was 32 cm on average. Every 24 hours was considered as one camera trap day for this study. The photographs were sorted manually and also with the help of Microsoft Access-based Camera Base 1.7 (Tobler 2015). The species from the photographs were identified with the help of the references from Sanderson and Watson (2011), Johnsingh and Manjrekar (2012) and Menon (2014), as well as consultation with experts and Forest Guardians from local villages who assisted with installing the camera traps. Photographs that were taken more than 30 minutes apart from each other were considered as independent events (Di Bitetti et al. 2006; Silver et al. 2004).

Results and discussions

Overall, there were 3,014 trap days (1,402 in winter and 1,612 in spring) from the 107 camera stations (52 in winter and 55 in spring) that collected 5,176 photographs of 17 medium-large sized mammal species. Of interest were three photos of a small felid (two whole body and one tail-only photo from its right flank) in a single event from a location ID W33 (27°20'2.22"N, 88°0'55.08"E; datum WGS84), (elevation: 2,750 m a.s.l.; aspect: west; slope: steep, details on Table 1) an dusk at 17:44 hr on 21 January 2018 (Figure 2). During the successive spring season (March-June), we surveyed the area where the marbled cat was detected intensively and systematically with seven monitoring stations. This resulted in 233 more camera days but with no more images of the marbled cat. One of the cameras was installed in previously trapped locations for a further 35 days.

The cat recorded location was near Tham Chok (a temporary shed for *dokpa*) from Phalaicha village in Panchthar District. The photos of the small felid were markedly different from other small cat images captured by other cameras in the area. A long, fluffy and erect tail, black edged large blotches on a flank and solid spots on the limbs were consistent with a marbled cat (confirmed by Igor Khorozyan, Jim Sanderson, Karan Shah, Kashmira Kakati, Rinjan Shrestha and Yadav Ghimirey). The camera trap images also matched (Figure 2) with published photos of the species (Dhendup et al. 2016; Nowell and Jackson 1996; Sethy et al. 2017). The marbled cat images clearly differed from the other felid species observed in this study, i.e. Asiatic golden cat, common leopard and leopard cat. The confirmation of the presence of the marbled cat at this site supports C. MacDougal's suggestion (Nowell and Jackson 1996) about the presence of the marbled cat in Nepal despite the lack of clear evidence about the origin of the cat's skin.

Table 1. Camera trap location details where the marbled cat was photographed in Southern Kangchenjunga region, eastern Nepal.

Parameter	Value
Location ID/Name of Location	W33/Tham Chok
Long/Lat	27°20'2.22"N, 88°0'55.08"E
Elevation	2,750 m
Total number of photos	3
No. of Independent events	1
Duration of camera placement	7–22 Jan 2018 (15 days)
Date, time & temperature of marbled cat recorded photo	21-01-2018, 17h 44m & 5°C
Habitat type	Upper-temperate mixed-broadleaved forest
Site aspect	West
Slope	Steep
Camera sensor height from ground	50 cm
Distance to nearest human settlement	1.4 km
Distance to nearest cattle herding station	0.4 km
Distance to forest edge	320 m
Distance to permanent water source	1 km
Distance to nearest forest in Sikkim, India	4 km
Distance to nearest trail for human & livestock	50 m
Other mammal species captured at the same camera	Orange-bellied Himalayan squirrel & Northern red muntjac
Bird species captured in the same camera	Kalij-pheasant
Species captured by the camera trap in same location in spring season	Leopard cat, Red muntjac, Yellow-throated marten and Wild boar

The habitat of the Tham Chok area is upper-temperate broadleaved forest (Figure 3). The vegetation in the area is dominated by *Lithocarpus pachyphylla*, *Castanopsis hysterix*, *Rhododendron grande*, *Taxus wallichiana*, *Lyonia ovalifolia* and *Alnus nepalensis* with thickets of *Arundinaria* sp. The recorded site is close to the Iwaa River, which originates from Timbung Lake at 4,200 m a.s.l.. The ridge is just above the confluence of Iwaa and Barne Rivers, which stretch towards the border with India, approximately 4 kilometres (km) away. The area is a summer grazing pasture for cows and goats and also a winter grazing pasture for dzomu (domestic yak-cow hybrids), supporting around 150 livestock over the winter. The eastern part of the Tham Chok is a largely rocky area with dwarf trees, probably recovering from a historical forest fire. A large area of primary forest in the Iwaa valley was burnt by a forest fire, presumably caused by incidental poachers, approximately 3.5 decades ago (pers. comm. K. Bhandari 2018). That forest fire caused huge damage to the local fauna and flora at that time. The habitat area is crisscrossed by human and livestock trails. A human trail was 50 m away from the camera trap station that recorded the marbled cat. The elevation record of the species in this study at 2,750 m a.s.l. is higher than the elevation limit of the species for Nepal (< 2,500 m a.s.l.) presented by Baral and Shah (2008). Despite a heavy presence of humans and livestock in the area, there is some pristine primary forest dominated by *Lithocarpus pachyphylla*, *Castanopsis hysterix*, and *Rhododendron* sp., in

Figure 2. An image of the first marbled cat in Nepal from the camera trap (Sonam Tashi Lama-Lincoln University/Red Panda Network).

the eastern portion of the area, approximately 2.5 km away. That primary forest could be a refuge habitat for many wildlife species, including small and medium-sized felids.

The other mammal and bird species captured at the same camera trap were the northern red muntjac *Muntiacus vaginalis*, orange-bellied Himalayan squirrel *Dremomys lokriah* and the Kalij pheasant *Lophura leucomelanos*. Similarly, leopard cat, yellow-throated marten *Martes flavigula* and wild boar *Sus scrofa* were recorded in the spring season. The photo-capture rate for that camera was highest for the muntjac followed by the squirrel in winter. The main prey present in the area, the orange-bellied squirrels (Figure 4) (Nowell and Jackson 1996) were also found to be strongly diurnal of habit in this study. Our images also support that marbled cat was primarily diurnal in their habit (Figure 2) as many other records around the world. A nearby camera trap, approximately 1 km away, only captured the photographs of dzomus, indicating the pressure of livestock in the area.

Marbled cat appear to have a very low capture rate throughout their range. The reason behind the low rate of the capture of the species could be due to the rareness of the species itself (Nowell and Jackson 1996; Azlan and Sharma 2006; Cheyne and Macdonald 2010). Failure to record the marbled cat during the spring season, despite intensive sampling of locations, may also indicate the rareness of the species in our study area or that we missed them because all of our cameras were based on the

Figure 3. The landscape and forests of the marbled cat capture area in Iwaa valley. The cat was photographed at far right (marked with red oval). (Sonam Tashi Lama-Lincoln University/Red Panda Network).

ground and they can be arboreal in nature (Sunquist and Sunquist 2017). Azlan and Sharma (2006) also reported a very low abundance of marbled cat (only one photo) and suggested that the cat could be rare and/or are mostly arboreal. Cheyne and Macdonald (2010), in Sabangau peat-swamp forest, Indonesian Borneo, did succeed in trapping a single image of this cat over 15 months, which further suggests the rarity of this species in the natural habitat. Camera-trap images of the marbled cat and the leopard cat were shown to nine *dokpa* in the first week of October 2018 and asked if they had sighted the cat in their area. Four of *dokpa* reported sighting the marbled cat, but all of them named it as a *chari bagh* (leopard cat). They understood them as a poultry pest that sometimes preys on goats. They had knowledge of the use of marbled cat skin and bones.

In a study by Hearn et al. (2016), the marbled cat was recorded from selectively logged area to primary forests but was not recorded inside the plantation forest. Their study estimated the density of the cat as higher than the Sunda clouded leopard *Neofolis diardi* and quite similar to the estimate of the leopard cat. In our study, the record of the leopard cat was relatively high.

The records of a marbled cat skull by Pocock (1939) from adjoining Darjeeling, India and one skin record originating from Sikkim, indicate that the cats were present in the region decades ago. This was also supported by the recent camera-trapped marbled

Figure 4. The Orange-bellied Himalayan squirrel *Dremomys lokriah*, a probable primary prey of marbled cat, is abundant in the study area. This individual was captured by the same camera trap (Sonam Tashi Lama-Lincoln University/Red Panda Network).

cat in Sikkim, adjoining and contiguous to our study area (pers. comm. P. S. Ghose 2018). This is consistent with the specimen collected by Hodgson from Nepal and the listing this species in the Nepal list by Horsfield (1856).

Hodgson was not allowed to travel outside of Kathmandu Valley during his stay in Nepal but he recruited a team of hunters and trappers to collect specimens for him (Datta and Inskipp 2004). He also did the same during his time (1845–1858) in Darjeeling, India (Hunter 1896) and his four assistants (bird and animal shooters, collector and taxidermist) travelled to eastern Nepal from October through to December 1948 with Sir Josheph Dalton Hooker (Hooker 1889). Due to the requests from the Lamas of Buddhists monasteries not to shoot or even fish in their surroundings (Hunter 1896), this might have limited the collection. On the other hand, some local ethnic people in eastern Nepal worked as licensed hunters for four generations to British India to hunt and trap birds and mammals for collections (pers. comm. S. B. Rai 2017).

The forest area, where the marbled cat was detected, has been naturally restored as a secondary forest after a forest fire that occurred nearly 3.5 decades ago. The slash-and-burn agriculture system was practised in the adjoining areas for many years until around 1998 (pers. comm. K. Bhandari 2018). The ongoing restoration of the secondary forests supports healthy biodiversity, including the top predators and provides

opportunities for combining forest regeneration and sustainable rural livelihoods for local people (Chazdon 2008). After banning grazing in the forest and removing mobile pastoralism in Sikkim in 1998 and Singhalila in 1992, the pressure of livestock has concentrated into the study area (Thomas 2014). The current number of livestock (cow, buffalo, yak, sheep and goat) in surrounding villages (Phalaicha and Kalikhola only) is 6,472 (MoLD 2017), of which at least 50% of them are grazing freely in nearby forests.

Small cats have been little studied in Nepal (Thapa 2014). The conflict between humans and marbled cat throughout its range appears to be low (Inskipp and Zimmermann 2009). It is not clear whether the low level of knowledge about the marbled cat throughout its range is due to rarity or its solitary and cryptic nature as a species (Sunquist and Sunquist 2017). In this context of limited knowledge on its ecology, distribution and status on a global level (Ross et al. 2016), we stress further research for gathering baseline data and appeal for conservation programmes outside the protected areas of Nepal. We expect to find the presence of the marbled cat in KCA, Makalu Barun National Park and most of the forested areas in the mid-hills of Nepal as the habitat and climates are similar to where we photographed the cat in eastern Nepal. As the coverage of forested areas by a camera-trapping survey in western Nepal is very low and limited to the protected areas, we cannot definitively conclude its absence from that region.

Based on a single presence location recorded in this study, it would be impractical to conclude anything about habitat characteristics for the marbled cat in Nepal. Limited information on population ecology, interactions with other sympatric felids, as well as how the species responds with the growing anthropogenic interactions in human-dominated landscapes, does not allow for an effective conservation plan. Nevertheless, the record of this species within a human-dominated landscape underpins the need for wildlife-friendly conservation measures to secure human-wildlife coexistence. Potential habitat identification following habitat zonation measures will help limit human activities outside the core habitat thus minimising the threat to some extent. However, an in-depth study on habitat characteristics, diet, distribution, movement and activity pattern will further guide in formulating an effective conservation plan targeting this species.

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RESEARCH ARTICLE

Unique botanical values in a metropolitan area and the landscape history reasons of their occurrence on the Széchenyi Hill, Budapest

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Abstract

Urban areas host several threatened species in small reserves that face habitat loss and fragmentation due to land-use change. Despite historical and current disturbances, these areas sometimes still maintain high biological diversity. As only 5% of the European Union territory was classified as natural, the permanent grasslands represent overriding value, especially in metropolitan areas. Our aim was to explore protected and adventive plant species in a small and valuable, but till now, not deeply studied area of the densely inhabited 12th district in the metropolitan city Budapest (Hungary), which is visited by large numbers of people. We compared various historical map sources in order to explain how the extension of the grasslands has changed during the past centuries and, thus, which patches are permanent grassland habitats. We found 29 protected and 1 strictly protected plant species. The highest number of protected plant species and their stands were found in the permanent grasslands. Besides urbanisation, a heavy load of tourism (especially on non-designated routes), off-road mountain biking, airsoft races, some illegal shelters for homeless people and game damage threaten this unique refuge of high natural values. The extension of grasslands between 1783 and 2016 varies from 6.7 ha to 21.5 ha. Their area constantly increased due to deforestation until 1867 and exceeded 20 ha, probably due to the mass increase in livestock grazing; then it stagnated until the 1920s, with a slight decrease due to expanding urban areas. Golf greens appeared, walker and skiing tourism increased and these apparently have not decreased the coverage of grasslands, but surely affected the composition of their species. Recent scrub encroachment and re-forestation caused a further decrease. Our distribution maps show the highest density of protected plant species on the

southern slopes (2.4 hectare) that have constantly been grasslands since 1783 to date. Contrarily, the cutting of grasslands from 1861 to date contains only half of their number per area unit. Thus, the number of valuable plant specimens refers to the age of the grassland. Three species occur only in the oldest grasslands. Conservation actions should first and foremost focus on these patches.

Keywords
Adventive plant, conservation, environmental history, grassland, protected plant, protected area management, urban areas

Introduction

Urban areas occupy less than 0.5% of the Earth's total land area (Schneider et al. 2009), yet they might host several protected and threatened species (Ives et al. 2016; Kowarik 2011). These values often occur in small, fragmented reserves that are the outcome of complex social and political processes (Williams et al. 2005). The main reason for this is that urbanisation is a significant land-use change that leads to habitat loss and fragmentation (Seto et al. 2012) and cities are often located in areas of high biological diversity (Luck 2007). Plant conservation biologists have shown that, even in the urban regions, there may also exist a large proportion of threatened or rare species (Kendle and Forbes 1997; Godefroid 2001). Twenty-two per cent of the known occurrences of endangered plants in the USA fall within the 40 largest cities (Schwartz et al. 2002). A total of 48 per cent of the 962 highly threatened taxa in California is restricted to high and medium density counties (Schwartz et al. 2006). Rapidly changing cities pose a threat and a challenge to the continuity that has helped to support biodiversity (Andersson and Barthel 2016). Therefore, more attention and conservation efforts must be focused on urbanised and urbanising regions (Rosenzweig 2003).

The effectiveness of different-sized reserves has been studied for about a century, with early warnings on the positive relationship between species richness and area (Arrhenius 1921). Although several studies proved the importance of small conservation reserves (e.g. Shafer 1995), the designation of protected areas remote from cities remains the dominant conservation paradigm world-wide (Miller and Hobbs 2002). The active protection of small sites is a challenging task for nature conservation, as smaller areas suffer more from human disturbance, pollution and other negative effects coming from the surrounding matrix (Deák et al. 2016). Kendal et al. (2017) found, in their floristic survey of 68 urban grassland conservation reserves, that 87% of all native plant species were found in small reserves < 10 ha in size, more small reserves containing a greater number of species than the few large reserves of a comparable area. Small reserves can also contribute to conservation at a landscape level by providing stepping stones between larger reserves which contribute to meta-population dynamics (Dearborn and Kark 2009). In favour of keeping the biodiversity in metropolitan areas, the complexity of the land mosaic should be preserved, especially within the urban matrix (Capotorti et al. 2013, Hüse et al. 2016). The history of urbanisation affects contemporary urban vegetation assemblages. This indicates potential extinction debts, which

have important consequences for biodiversity conservation planning and sustainable future scenarios (du Toit et al. 2016).

The flora of Hungary's state capital, Budapest, has been investigated since the 18th century. However, constant changes justify regular monitoring of protected species to recognise threats as well. Our aim was to prepare distribution maps of protected and adventive plant species in a small and valuable, but till now, not deeply studied area of the densely inhabited 12th district in the metropolitan city Budapest, visited by great numbers of people. We also aimed to explain how these unique species could survive despite anthropogenic effects (including land use change, expansion of built-up areas) through millennia and constant disturbance (including inhabitation and urbanisation). Seeing that the majority of protected species are hosted by grassland habitats, we explored the landscape history, in order to explain how the extension of the grasslands has changed during the past centuries and, thus, which patches are permanent grassland habitats and whether the greatest number of protected plant specimens overlaps with the permanent grasslands.

Geography and climate of the study area

The Széchenyi Hill (472 m above sea level) belongs to the Buda Hills (top peak 529 m a.s.l.). The study area is situated in the central part and southern slopes of the Széchenyi Hill and mainly covered by grasslands, although our investigations included the surrounding forested habitats as well (Figures 1, 2). Dominant basal rock is dolomite (from Upper Triassic), with a smaller ratio of Triassic limestone and freshwater limestone from the late Pliocene. During Pleistocene glacial periods, the area was not covered by ice, but affected by nearby ice sheets.

The climate is moderately cool and moderately dry. Due to rainfall distribution, it exhibits a submediterranean character. The hill occupies a transitional position between lowlands and mountains, due to the closeness of the Great Plain and the Danube. Sunny hours reach 1930 per year. Its climate is colder than the average in Budapest, with 8.7 °C annual mean temperature. Winter temperature inversion is a frequent phenomenon here: unclouded, sunny hilltops are even 10 °C warmer than valleys and lowlands in the city. Annual rainfall exceeds 650–700 mm, the most during early summer, the least around late winter. Snow cover lasts for 50 to 55 days. Rendzina soil is dominant on the surface. There are no springs on the Széchenyi Hill (Dövényi 2010).

History

According to the first written documents, which date back to the 12th century, wine cultivation had started after deforestation. Wine production slightly decreased during the Ottoman invasion and flourished again in the 18th century, but was ended by the phylloxera infestation (late 19th c.). Cottages and chalets replaced the wine plantations (Siklóssy 1929).
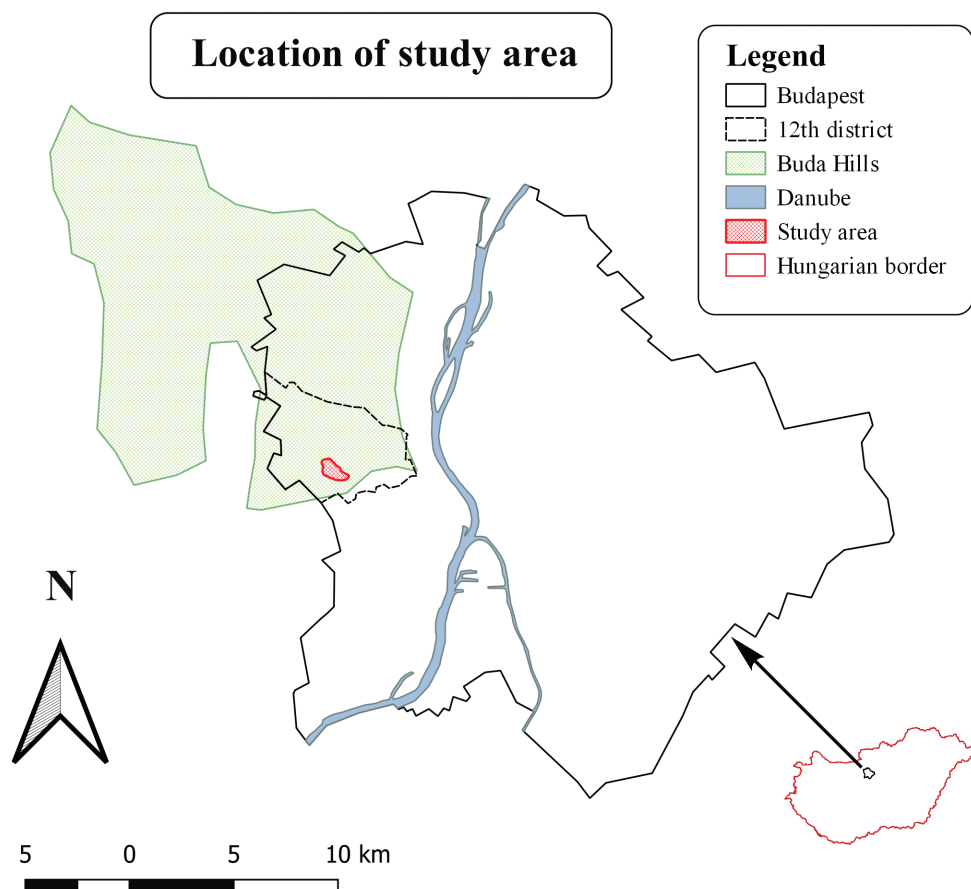
Figure 1. Location of the study area.

The process of urban citizens settling in the surroundings during the 19th century encouraged the development of public transportation. A cog-wheel railway has been running from the city-centre up to the Széchenyi Hill since 1890, giving opportunity for the development of a new district, increasing population and growing the number of tourists. New forests were planted (partly of adventive trees), recreational sites were built and touristic routes were designated. Even ski tourism has flourished after 1920 on the hill. Ten tourist hotels were built in the vicinity between 1939 and 1943, some of them at the border of the valuable grasslands. The Hungarian Golf Club was launched here in 1910, with a high-standard golfcourse and fairways which was declared the second most beautiful in Europe by a British golf magazine (Siklóssy 1929). Economic growth stopped during the two world wars, which caused serious harm to the natural values, since both airborne bombings and land battles affected the area. After World War II, a small-gauge railway (operated by pioneers in the Soviet times) started to operate, with a terminal station (and several buildings) at the border of the valuable grasslands. At the same time, the golfcourse and fairways were abandoned, their place

now being covered by secondary grasslands, railway tracks and a military base. The 56-m high main television tower of Budapest was built directly on to the grassland (at the border of the study area) in 1958, completed with a 150 m high steel tower in 1973.

Official nature protection was launched in 1978 by the Buda Landscape Park, which surrounds Budapest from the north-west. Since Hungary's EU-accession (2004), the study area is also covered by the Natura 2000 ecological network.

Vegetation

Original Holocene vegetation of the area has evolved during the past 10 to 12 thousand years, with relict species remaining in forests and rock grasslands. Besides the climate, anthropogenic activities played a significant role. Original, ancient vegetation was probably intact until the Roman imperial age. The greatest changes have occurred since the mid-19th century, giving home to cultivated plants and weeds (Pénzes 1942).

High plant diversity of the Buda Hills is a consequence of its geographical situation (mix of plain, lowland, hillside), various geomorphology and micro-climatic conditions. It belongs to the Pilisense floristic district within the Bakonyicum floristic sector (part of the Pannonicum floristic region) (Fekete et al. 2017) and hosts both northern and southern species and even endemisms, such as *Linum dolomiticum*. Southern surfaces of the Széchenyi Hill are covered by Pannonian karst white oak – manna ash low woods.

During his floristical studies in 1818, József Sadler recognised that Budapest hosts several rare species and diverse habitats. Vince Borbás stated in 1879 that the vegetation of Budapest significantly differs from the Central European vegetation due to southern and eastern floristical elements. He mentions *Anthericum liliago*, *Amygdalus nana*, *Coronilla coronata*, *Iris pumila* and *Lathyrus pallescens* from the Széchenyi Hill (Pénzes 1942). Somlyay (2009) presents the main features of floristical phytogeography of the Buda Mts. based on local distribution pattern of several species with phytogeographical relevance. He mentions *Amygdalus nana* and *Phlomis tuberosa* as oriental species with evident migration routes through the Pannonian lowlands, while *Coronilla coronata* and *Crepis nicaeensis* as sub-Mediterranean species. Tamás et al. (2017b) has recently reported rare ferns from adjacent areas.

Materials and methods

Impoundment of the study area

The study area was designated based on satellite photos and detailed field surveys (Figure 2).

Investigations were undertaken in 2015 and 2016, every 2 to 4 weeks during the vegetation period. The central grassland designated for systematic research covers 8.5 hectare. The surrounding low woods, which were designated based on satellite photos
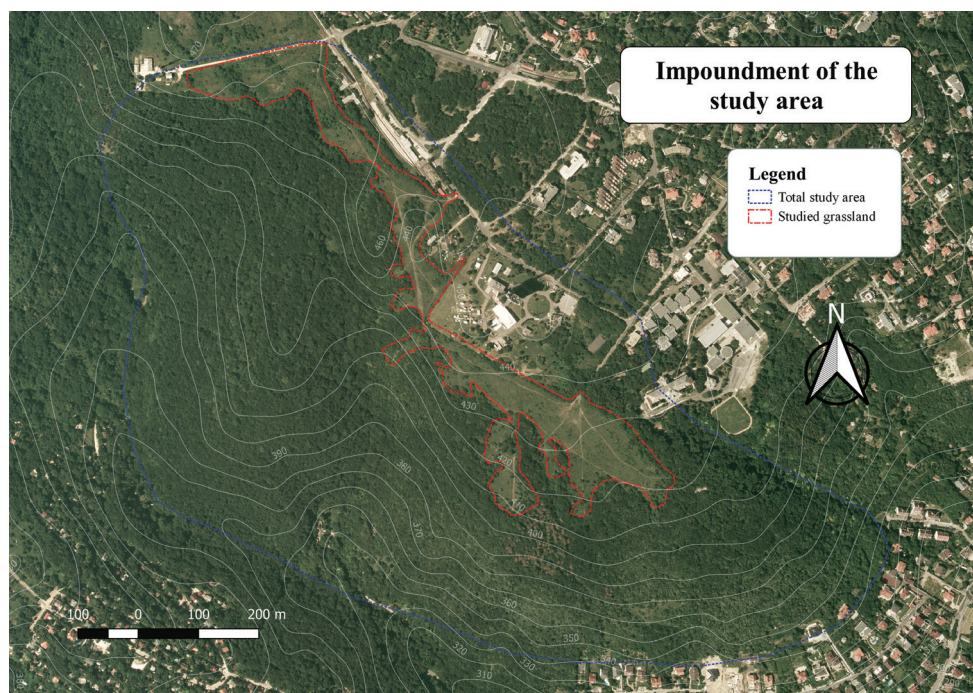
Figure 2. Impoundment of the study area (based on Google Earth satellite photos).

and cover 77.5 ha, was observed occasionally, but is also important for historical reconstructions. We strived to soundly rake over the whole area (with 'rambling method') during every visit and recorded the GPS coordinates in case of protected plants; while the other (non-protected) species were listed.

Division of individual plant specimens

Plants were determined with the help of the determination book of Király (2009). Division of individuals was not easy in many cases, due to various reasons. As several species create polycormons (e.g. *Lathyrus pallescens, Iris pumila*), we, therefore, decided to record two sets of data in the case of each protected taxon, the number of flowering stems and the number of stands. Determination of the latter was difficult, so we counted those stems as one patch that apparently form one stand. We used the same method in case of several non-polycormon species as well, if the stems grew so densely that made the division of each specimen impossible (e.g. in the case of *Polygala major*).

Landscape history research methods

Besides archive literature, our bases for the landscape history research were military maps and aerial photos, online maps of the mapire.eu and Google Earth and recent

online aerial photographs from the Department of Geodesy, Remote Sensing and Land Offices, Hungary (for the list of sources, see Table 2). We have processed them with Quantum GIS software and impounded the grassland area with polygons. The most reliable data amongst them were the aerial photographs, while the maps were inaccurate in most cases, especially the First Military Survey (Molnár et al. 2014); georeferencing is aggravated by the lack of signed objects or landmarks that would provide suitable points of reference. In the case of recent maps and aerial photographs, the number of points of reference has been increasing and, thus, these are more accurate.

In order to answer the research question how the extension of the grasslands has changed during the past centuries and, thus, which patches are permanent grassland habitats, we impounded those areas that are indicated on the map as (or seem to be) grasslands and worked with the profile of the polygons generated by this method. In order to minimise the errors that emerge from inaccuracy, we marked a buffer zone around the designated grasslands in line with the inaccuracy rate of the map (10, 15 and 25 m). These are just approximate data, presumed on the basis of the deviation of georeferenced points from their real location and the distances between the fitting of the segments.

Results and discussion

We found 29 protected (one of them is Natura 2000 Annex species) and 1 strictly protected plant species in the grasslands and forests of the studied area (Table 1). With regard to the fact that exact number of specimens cannot be determined in every case (due to the reason presented in *Division of individual plant specimens*), the nature conservation value is provided based on the number of stands (see Suppl. material 1); thus, this is a minimum value, the real value being probably higher. The sum value of protected plants still exceeds 300,000 Euro and most of their stands are located within the mere 8.5 hectare grassland. Based in this, it is obvious that the grassland of the Széchenyi Hill covers an outstanding value. An aggregated distribution map of all protected species is presented in Figure 5.

Adventive elements (and amongst them, invasive alien species) are rare in the area, despite the fact that human population density surrounding protected areas is a significant and strong predictor of numbers of alien and invasive species (Spear et al. 2013). Tree of Heaven (*Ailanthus altissima*) is the most aggressive amongst them, but only 6 specimens were fortunately found so far. Other invasive alien species are, fortunately, rare in the area as well, such as Canadian horseweed (*Conyza canadensis*), fleabane (*Erigeron annuus*), Oregon-grape (*Mahonia aquifolium*), goldenrods (*Solidago canadensis*, *S. gigantea*) and non-invasive, but still adventive yew (*Taxus baccata*). Former surveys did not mention adventive or invasive alien species from the Széchenyi Hill. Although these few stands of invasive alien species have not threatened protected values until now, some indigenous shrub species have caused undesirable processes and difficulties for nature conservation, such as common hawthorn (*Crataegus monogyna*) and sloe (*Prunus spinosa*). Their recent expansion in dry steppes is a consequence of the abandonment of traditional landscape management patterns and leads to re-forestation and disappearance of protected values.

Table 1. Protected plant species found on the Széchenyi Hill, Budapest (strictly protected species is indicated with an asterisk; Natura 2000 Annex species in bold).

Scientific name	Minimum number of stands
Aconitum vulparia	160
Adonis vernalis	274
Allium sphaerocephalon	609
Amygdalus nana	30
Anemone sylvestris	15
Aster amellus	40
Asyneuma canescens	220
Centaurea scabiosa subsp. *sadleriana*	3280
Centaurea triumfettii	87
Cephalanthera damasonium	27
Convolvulus cantabrica	78
Coronilla coronata	165
Crepis nicaeensis	29
Dictamnus albus	1072
Erysimum odoratum	442
Iris pumila	903
Iris variegata	6
Jurinea mollis	246
*Lathyrus pallescens**	163
Limodorum abortivum	91
Linum flavum	12
Linum tenuifolium	327
Lychnis coronaria	49
Orchis purpurea	28
Phlomis tuberosa	21
Polygala major	495
Pulsatilla grandis	846
Scorzonera purpurea	60
Sorbus danubialis	8
Vinca herbacea	1952
SUM	11 735

Historical changes of the grasslands

Changes in the extension of grasslands on the Széchenyi Hill between 1783 and 2016 vary from 6.7 ha to 21.5 ha (Table 2). No data are available for the beginning of the first period, but presumably coincides with the population boom after the Liberation War 1703-1711 and lasts until 1867 (Austrian-Hungarian Conciliation). During this period, the area of grasslands constantly increased due to deforestation and finally exceeded 20 hectares, probably due to the mass increase in grazing livestock in parallel with the population boom. Coverage of grasslands stagnated until the 1920s, with a slight decrease due to expanding urban areas. Golf fairways and greens appeared during and after this period, in line with increasing tourism (both walker and skiing), which apparently have not decreased the coverage of grasslands, but surely have affected their species composition.

Table 2. Extension of grasslands on the Széchenyi Hill (1783–2016).

Year	Source of data	Area of grassland (m²)
1783	First Military Survey Map	118273
1861	Second Military Survey Map	153079
1873	Cadastre Maps of Buda	214520
1882	Third Military Survey Map	213585
1923	Renewed Third Military Survey Map	206760
1955	Aerial photograph of the Military History Map Archives	165728
1959	Renwed Gauss-Krüger projection map	127045
1978	Aerial photograph of the Military History Map Archives	108172
1987	Aerial photograph of the Military History Map Archives	106315
2004	Google Earth satellite image	81366
2016	Google Earth satellite image	67773
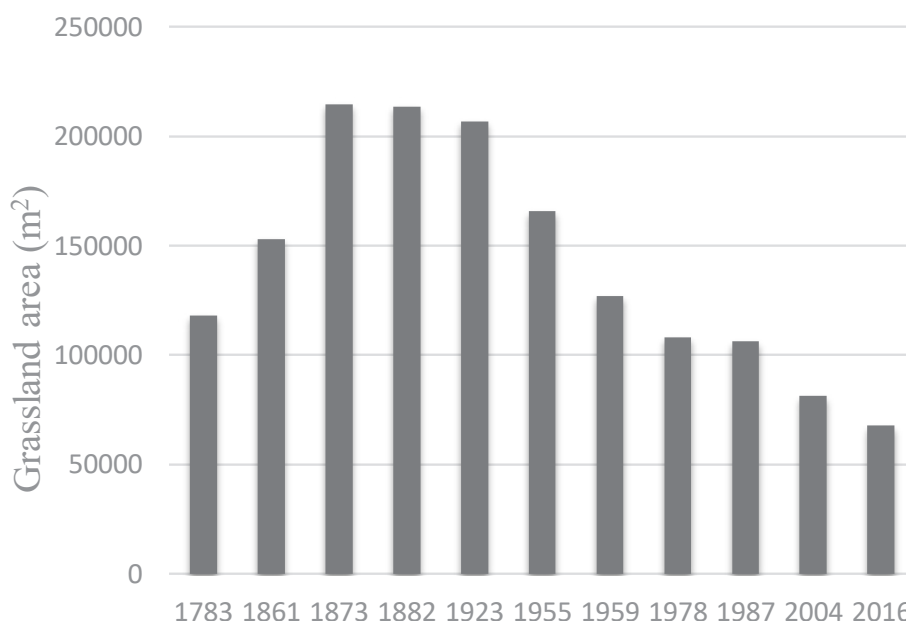
Figure 3. Changes in the extension of grasslands on the Széchenyi Hill (Budapest) from 1783 till 2016.

Creation of the Children's (that time: Pioneers') Railway and the national television broadcasting tower during the 1950s caused a massive fall in grasslands, followed by a slighter decrease until the change of political regime (1989) due to slow scrub encroachment and creation of military bases. A possible reason for this fall-off might be the declaration of the Buda Landscape park in 1978, covering also the Széchenyi Hill.

The past three decades showed another massive fall in the extension of grasslands, due to scrub encroachment and re-forestation caused by the abandonment of traditional management (but no data are available for previous management forms) (Figure 3). The current rate of decrease in grassy areas is very close to the coverage of presumed permanent grasslands.
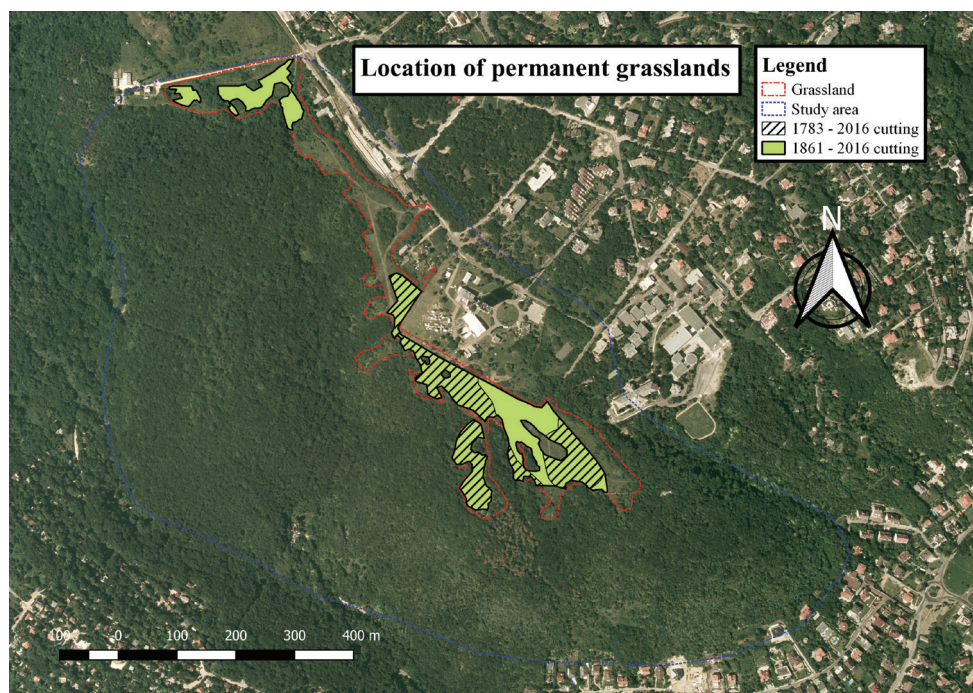
Figure 4. Presumed location of permanent grasslands on the Széchenyi Hill, Budapest.

Determination of the permanent grasslands

Permanent grasslands, i. e. those areas that have constantly been covered by grasslands (instead of forests) during the past 235 years on the basis of a cutting of historical maps, aerial photographs and satellite images, are presented in Figure 4. With regard to the relatively high inaccuracy of the First Military Survey Map (as the earliest source) and the difficulties of georeferencing due to the low number of reference points, we also prepared another cutting based on data of the past 150 years (i.e. since the Second Military Survey Map of 1861). Figure 4 shows that dominant parts of the permanent grasslands cover the southern slopes, while a small patch can be seen on the northern plateau. Our distribution maps show the highest density of protected plant species on the southern slopes, while the latter patch hosts almost none of them. A possible explanation for this phenomenon is that this patch belonged to the central part of the golf green and fairway during the 1930s and was affected by sown grass seeds (imported from England) besides trampling, which probably caused a massive shift in species composition.

The total area of permanent grasslands since 1783 to date is 24,056 m^2, while the same data since 1861 is 54,128 m^2, dominated by southern slope steppe grasslands of rocky weak soils in both cases. The greatest number of protected plant specimens per area unit can be found on those patches that have constantly been grasslands
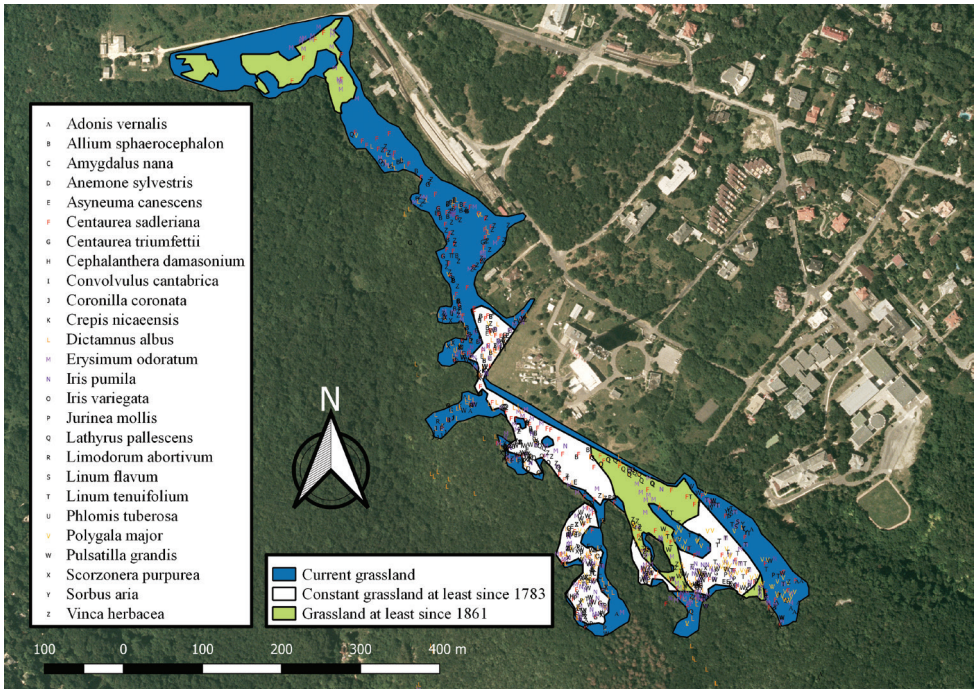
A Adonis vernalis
B Allium sphaerocephalon
C Amygdalus nana
D Anemone sylvestris
E Asyneuma canescens
F Centaurea sadleriana
G Centaurea triumfettii
H Cephalanthera damasonium
I Convolvulus cantabrica
J Coronilla coronata
K Crepis nicaeensis
L Dictamnus albus
M Erysimum odoratum
N Iris pumila
O Iris variegata
P Jurinea mollis
Q Lathyrus pallescens
R Limodorum abortivum
S Linum flavum
T Linum tenuifolium
U Phlomis tuberosa
V Polygala major
W Pulsatilla grandis
X Scorzonera purpurea
Y Sorbus aria
Z Vinca herbacea

■ Current grassland
□ Constant grassland at least since 1783
■ Grassland at least since 1861

Figure 5. Protected plant species are most abundant in permanent grasslands (letter colors serve better visibility).

Table 3. Rate of protected plant species on permanent (and total) grassland areas of the Széchenyi Hill.

Studied area	Species number	Flowering stem	Number of stands	Area (m²)	Ratio of flowering stem / area
1783 – 2016 cutting	22	15863	5117	24056	0.659
1861 – 2016 cutting	21	18834	6079	54128	0.348
Grassland in 2016	21	29997	10426	67773	0.443

since 1783 to date. Contrarily, the cutting of grasslands from 1861 to date contains only half of their number per area unit. A possible reason for this is that the newer grasslands cover mainly those areas that previously have been used for golf purposes or are situated in the central part of the current lawn and, thus, are affected by heavy trampling (Table 3).

The highest number of protected plant species, as well as the highest number of their stands, was found in the permanent grasslands (Figure 5). Thus, the number of valuable plants refers to the age of the grassland. Moreover, *Amygdalus nana*, *Crepis nicaeensis* and *Phlomis tuberosa* occur only in the oldest patches, while those species that spread slowly, such as *Iris pumila*, are most abundant in the oldest grasslands as well. *Anemone sylvestris* and *Coronilla coronata* appear at the edges of younger grassland patches surrounded by Pannonian karst white oak – manna ash low woods. *Limodo-*

rum abortivum and *Sorbus aria* are indicators of re-forestation on the younger parts. Some other protected plant species that we found, such as *Aconitum vulparia* and *Lychnis coronaria*, occur only in the surrounding forests close to the grasslands, while we have not recorded *Inula oculus-christi* and *Thlaspi jankae* in the years of our investigations, but only in the following year (2017); this is the reason we do not show them on Figure 5.

Conclusions

Hegedüs (2002) concluded by his thorough examinations that 341 plant species have disappeared from the flora of Budapest during the past 100 years, primarily due to urbanisation. This trend calls for regular and systematic monitoring of the flora, especially in case of protected species. The 29 protected and one strictly protected plant species (which has only one more location in Hungary) that we found, prove this area to be recognised as of extraordinarily rich in natural values, even in an international comparison. For example, Feráková and Jarolímek (2011) list 7 taxa that have their only occurrence in Slovakia in Bratislava and 7 Natura 2000 taxa; while Sofia's flora includes 12 statutorily protected species (Dimitrov et al. 2011) and 60 species were recorded in Warsaw that are protected by Polish law (Sudnik-Wójcikowska and Galera 2011). Half of the flora of Belgium, Germany and The Netherlands occur in Brussels, Berlin and Maastricht, respectively. A possible reason for the high biodiversity of European cities is that they have been established along landscape transition zones and rivers in regions that are naturally highly heterogeneous in terms of their landscape (Müller 2011).

Although the studied area belongs to the Buda Landscape Park, its real protection and conservation is complicated, since touristic routes lead through and is easily reachable, even by public transport. Besides urbanisation processes (i.e. expansion of built-up areas), the heavy load of tourism (especially on non-designated routes), airsoft races, some illegal shelters for homeless people and game damage (recent study from an adjacent area by Tamás et al. 2017a) threaten this unique refuge of high natural values. As soil loss is definitely larger on the steeper and longer slopes (Centeri and Pataki 2003; Centeri et al. 2015), illegal off-road mountain biking should be stopped at least in the valuable grassland patches.

Lack of information boards or fences refers to undesirably little attention being paid by nature conservation authorities. A key challenge for preserving biodiversity is balancing human perceptions, needs and use with ecological requirements (Aronson et al. 2017). By raising attention of the visitors towards unique species and spots with listing of the rules when entering protected areas and fencing the most vulnerable vegetation stands (either with wooden fence or by managing stinger shrubs such as hawthorn and sloe stands), in parallel with fighting against scrub encroachment and invasive alien species, the botanical values can be preserved in the long term. Although common hawthorn threatens the strictly protected *Lathyrus pallescens* stands, its elimination might aggravate degradation from human trampling, therefore, these interven-

tions should be thoroughly planned. The area also plays an important role in connecting people to nature, generating support for conservation and providing opportunities for education (Soga and Gaston 2016).

Taking into account that only 5% of the European Union territory was classified by the European Commission as natural (Agnoletti and Rotherham 2015), permanent grasslands represent overriding value, especially in metropolitan areas. Our studies reveal that about 2.4 hectare permanent grassland remained on the Széchenyi Hill, giving home to the greatest number of protected plant specimens per area unit within the 8.5 ha grassland. Conservation actions should first and foremost focus on these patches. Our case shows that urban areas contain a wide range of biodiversity (Farinha-Marques et al. 2017) and the value of urban ecosystems is very high due to interaction of human, social, built and natural capital (Sutton and Anderson 2016). We could support the statement of Kendal et al. (2017) that, while the theory and evidence showing the conservation benefits of large reserves over small reserves for some organisms is clear, small urban conservation reserves can make a substantial and genuine contribution to regional conservation outcomes. We confirm the argument of Duhme and Pauleit (1998) that special attention for biodiversity conservation in central Europe has to be paid to the urban landscapes because of their high importance for nature conservation and species richness. Flora and vegetation of the Széchenyi Hill meet the synthesised set of ecological and biological criteria of Asaad et al. (2017) and, thus, we identify it of high biodiversity significance.

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Supplementary material 1

Main data of protected plant species found on the Széchenyi Hill, Budapest
Authors: Károly Menyhért Nagy, Ákos Malatinszky
Data type: (measurement/occurrence/multimedia/etc.)
Explanation note: Value in Euro is based on the relevant law that determines it in Hungarian Forint.
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REVIEW ARTICLE

An evaluation of destination attractiveness for nature-based tourism: Recommendations for the management of national parks in Vietnam

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Abstract

National parks are increasingly recognized as playing an important role in the development of nature-based tourism destinations that promote effective management of natural resources and socioeconomic development. The paper was designed to evaluate the tourism attractiveness and performance of national parks in Vietnam. The tourism performance of 30 Vietnamese national parks was evaluated using multiple criteria decision analysis with the stochastic multicriteria acceptability analysis (SMAA) and preference ranking organization method for enrichment evaluation (PROMETHEE) method; thirteen national park attributes were used to determine tourism attractiveness, measured by an exponential weighted acceptability index. It was found that the Phong Nha – Ke Bang, Cuc Phuong, and Ba Be National Parks were most attractive for more than 95% of all possible preference structures. In addition, 12 non-dominated national parks were identified, and for an average supporter of most non-dominated protected areas, the trail criterion appears to be the most important. A statistically significant correlation was found between tourism attractiveness and the number of tourists who visited national parks. Our findings offer potentially useful information for decision makers in developing effective tourism marketing and management strategies for national parks in Vietnam.

Introduction

Nature-based tourism (NBT), also known as ecotourism or nature tourism, defined as travel to enable the enjoyment of undeveloped natural areas, is a rapidly-expanding area in the tourism travel sector (Luzar et al. 1995, Goodwin 1996). Most nature-based tourism destinations are located in protected areas (Eagles et al. 2002, ICEM 2003, Spenceley et al. 2015) which attract large numbers of visitors: globally, terrestrial protected areas receive approximately eight billion visits per year (Balmford et al. 2015) and European national parks receive more than two billion visits annually (Schägner et al. 2016). Despite having a potentially negative influence on natural resources, affecting both the environment and the species within them (Steven et al. 2011), NBT could be a particularly effective tool in the conservation and management of protected areas. It can also bring potential social and economic benefits, such as funds for conservation and alternative livelihoods for local people (Bookbinder et al. 1998, Eagles et al. 2002, Balmford et al. 2009, Ballantyne et al. 2009). Many countries promote NBT in order to help them achieve their goals for both nature conservation and socioeconomic development, and for several countries such as Australia and New Zealand, NBT is considered a key component of export income (Eagles 2002)

In the Southeast Asia region, NBT is not only a high volume sector but also one that is growing rapidly. For example, Thailand's national parks receive over 13.2 million tourists per year, which is approximately 16% of all tourists visiting the country (Phumsathan 2010), and Indonesia's Komodo National Park sees an 18% mean increase of visitors every year (Erb 2015). For foreign tourists visiting the region, many countries such as Thailand and Vietnam have become popular destinations for NBT because they harbor extraordinary levels of ecosystems and magnificent natural scenery (American Museum of Natural History 2003). In contrast to general items of tourism activity, foreign tourists tend to be more interested in nature-based activities: about 51% of surveyed foreign tourists visiting the Association of Southeast Asian Nations (ASEAN) preferred nature-based adventure tourism (ASEAN Secretariat 2016).

In Vietnam, NBT is increasingly recognized as playing an important role in national development, particularly of the national tourism sector, and one that supports socioeconomic development in the rural areas surrounding the protected areas. Around 51% of the 9.5 million domestic tourists and 33% of 1.2 million foreign tourists in Vietnam took part in nature-based tourism in 1998 (Luong 1999), and 5–8% of foreign tourists visiting the countryalso participate in nature-based tours every year (Le Van Minh 2016). Innovation policies highlight the significant efforts made by the Vietnamese government to promote the development of NBT. In particular, the introduction of economic and political reforms under *Đổi Mới* has helped the tourism sector develop from scratch since 1986. The first master plan of tourism development, for the period 1995–2010, released in 1994, mentioned the potential for natural resources to

increase tourism; following this, NBT emerged officially as an important driving factor behind tourism development. The master plan up to 2020 views NBT as one of the key products of tourism contributing to national development (GoV 2013). In total, the Vietnamese government and their related bodies, public and private interests, domestic and foreign corporations, as well as local communities, are involved in various ways to enhance the development of NBT (Suntikul et al. 2010). However, Vietnam suffers from a lack of planning or strategies on the national level regarding NBT. National planning is also crucial in the management and development of NBT destinations such as protected areas, which enhance the country's tourist attractions, including its natural environments, biodiversity, cultures and ancient history (Jansen-Verbeke and Go 1995, Hung 1998, Hong et al. 2002, Le Van Minh 2016).

Vietnam's national parks (NPs) are protected areas in the national systems of special-use forests (SUFs), which are intended to protect nature. Other objectives include the protection of landscapes, cultural and historical sites, and the provision of recreation and tourism (GoV 2010). Since the first Vietnamese NP (Cuc Phuong NP) was established in 1962, their number had increased to 30 (1,077,236 ha, reaching ca. 3% of the total land area) by 2012 (MONRE 2014). According to the approved national planning system of SUFs, Vietnam will have 34 NPs up to 2020 (1.2 million ha, reaching ca. 4% of the total land area) (GoV 2014). The increasing number of NPs supports the conservation and sustainable development of natural resources in the SUFs (GoV 2014). Several ministries and agencies are involved in the governance of the protected areas; for example, the Ministry of Agriculture and Rural Development (MARD) and Provincial People's Committee (PPCs) have the responsibility for managing national parks (see An et al. 2018). In particular, together with MARD, the Ministry of Culture, Sport and Tourism guides and examines PPCs in the management of eco-tourist activities and promotes NPs as tourism destinations in the development of the tourism sector at a national level.

An area with special potential to acquire financial sources of funding for natural resource management in Vietnam is the use of NBT in NPs (An et al. 2018), which has been found to create alternative livelihoods for local people and support local socioeconomic development (Rugendyke and Son 2005, MONRE 2014). Effective protected area management encourages the expansion of benefits from NBT, particularly in the economic sphere (An et al. 2018) and NPs are attractive destinations for recreation and tourism. The total number of tourists visiting 11 NPs increased by over 17% in a single year, reaching 629,961 in 2010 (MONRE 2011). However, NBT is a competitive market and NPs have to offer high quality and unique environmental characteristics to succeed in tourism development. Many NPs suffer from a lack of any tourism development strategy in their management plans (An et al. 2018), and tourism facilities and services of protected areas (e.g. information services) are also limited (ICEM 2003). It is important to consider the characteristics of NPs and their potential value as attractive destinations for tourism development when implementing effective management strategies for protected areas and tourism, and encouraging the sustainable use of natural environment and resources. Protected area managers need to identify the attributes of NPs that induce tourism and set priorities for enhancing the

attractiveness of tourist destinations and increasing the tourist flow to protected areas. Furthermore, an evaluation of the attributes of individual NPs, and of other tourism destinations in protected areas, is required to form the basis of local, regional and national strategic planning for NBT development, to enable effective management and planning of nature-based tourism destinations, sustainable tourism and socioeconomic development in the country.

The attractiveness of a travel destination is simply the ability of an area to attract and satisfy prospective tourists (Mayo and Jarvis 1981). This ability is enhanced by destination attributes, which can be classified in a variety of ways (e.g. see Cooper et al. 1993, Buhalis 2000, Morrison 2013). Two major approaches can be used to identify improvements to destination attractiveness that focus on the physical features of the destination (e.g. Leiper 1990, Backman et al. 1991) or the psychology of consumers/tourists and the perceived ability of destinations to satisfy their individual needs (e.g. Formica and Uysal 2006, Hsu et al. 2009). These approaches are also known as supply and demand aspects for evaluating the attractiveness of tourism destinations (Backman et al. 1991, Formica and Uysal 2006). However, most nature-based studies focus on tourist demand rather than on tourist destinations (Deng et al. 2002). Therefore, the present study examines the supply of destinations as characteristics of NPs, with respect to tourism attractiveness. It is necessary to identify the attributes that prompt tourists to choose one destination over another. This knowledge could help destinations to allocate resources and prioritize the investment and development of their tourism areas, and enable such destinations to fulfill and retain their potential. Determining and evaluating the attributes of a destination that play key roles in attracting and satisfying tourists is also integral to its management and marketing policy, particularly those oriented towards tourism strategies and plans to target markets (Buhalis 2000, Kim and Perdue 2011).

Furthermore, different strategies for tourism destinations can be evaluated by the broad application of multiple criteria decision support methods such as the Analytic Hierarchy Process (AHP) (Deng et al. 2002, Hsu et al. 2009, Lee et al. 2010) or the preference ranking organization method for enrichment evaluation (PROMETHEE) (Michailidis and Chatzitheodoridis 2006, Kovačić 2010, Ranjan et al. 2016). During the decision-making process, decision makers rank a set of decision alternatives with multiple criteria and choose the best, or at least a satisfactory, choice according to their preferences. In most multiple criteria decision methods, the preferences of the decision maker are modeled by a set of parameters, with a key role being played by the weight given to each criterion. However, in many real-life situations, decision makers are not able to give exact preference information (weights), nor is it possible to gain access to the decision makers to collect information about their preferences. Most of the associated information is uncertain or imprecise to a certain degree, and even relevant information can sometimes be missing (Lahdelma et al. 2000, Öztürk et al. 2005, Ranjan et al. 2016). In addition, when evaluating the attractiveness of tourism destinations, it can also be difficult to obtain weights when no single decision maker exists who could provide the necessary information, and in cases where the preferences of all potential decision makers (e.g. tourists) must be considered.

In these cases, stochastic multicriteria acceptability analysis (SMAA) can be used, this being a family of multicriteria decision-aiding (MCDA) methods for problems where uncertainty (incomplete, imprecise, and uncertain information) is a significant issue (Tervonen and Figueira 2008, Lahdelma and Salminen 2010). In contrast to the classical MCDA method, the SMAA method considers the evaluation space of all possible parameters (in the context of weights) (Lahdelma et al. 1998), which determines the significance of the percentage contribution of all possible weight combinations to a particular object specific rank. In particular, it indicates the most preferred combination, based on rank acceptability index (Lahdelma and Salminen 2001).

The aim of this paper is to explore the attributes associated with tourism attractiveness, and evaluate the tourism performance of national parks in Vietnam using stochastic multicriteria acceptability analysis. More specifically, it assesses various attributes of NP-based tourism destinations and ranks NP destinations. The attractiveness of Vietnamese NPs as nature-based tourism destinations is evaluated by the SMAA and PROMETHEE methods. In addition, the correlation between tourism attractiveness and the number of tourists visiting NPs is assessed. The paper also discusses recommendations for NP management, particularly with regard to the attractiveness of nature-based tourism.

Materials and methods

Selection of attributes for evaluating the tourism attractiveness of national parks

Various attributes associated with specific types of tourist destinations influence the motivation to visit a NP and to enjoy it. In other words, the park in this sense is best viewed as a package of tourism facilities and services, composed of a number of multidimensional attributes that together determine its attractiveness to a particular individual in a given choice situation. Deng et al. (2002) group these attributes into the following five general categories: (1) tourism resources, (2) tourist facilities, (3) accessibility, (4) local communities, and (5) peripheral attractions. The unique attributes determining the attractiveness of a forest-based destination include the variety of natural resources, the diversity of cultural and historical assets, the availability of supporting tourism infrastructure, and the provision of information services and convenience facilities (Lee et al. 2010).

In the conceptualization described above, thirteen attributes (criteria) were selected to evaluate the attractiveness of 30 NPs in Vietnam (Figure 1, Table 1). The criteria were derived from previous studies regarding the tourism attractiveness of protected areas (e.g. Deng et al. 2002, Puustinen et al. 2009, Lee et al. 2010, Castro et al. 2015). The biological diversity and presence of rare species of plants and animals indicate the value of the natural resources or natural characteristics of a destination (Deng et al. 2002), which are considered the primary elements of its attractiveness (Lee et al. 2010). In addition, historical, cultural and spiritual sites within NPs constitute the cultural resources of a tourism destination (Deng et al. 2002, Lee et al. 2010). Other criteria

Figure 1. Distribution of the thirty Vietnamese national parks. Source: Adapted to IUCN and UNEP-WCMC (2017).

reflect the managerial and social characteristics of NPs towards tourism attractiveness. For example, amenities such as lodging (e.g. hotels) and recreation facilities (e.g. trails) allow tourists to satisfy their basic needs (Lee et al. 2010). The provision of such services is recognized as playing a significant role in encouraging tourists to partake in the

Table 1. Attributes for determining tourism attractiveness Vietnamese national parks.

Attribute	Description
International importance	Were the national park or national park areas specified under international designations (Ramsar Site, United Nations Educational, Scientific and Cultural Organisation World Heritage Sites and United Nations Educational, Scientific and Cultural Organisation Biosphere Reserve), yes/no?
Biodiversity of plants and animals	Number of species of plants and animals recognized in the national park
Rare plants and animals	Number of species of plants and animals recognized in the national park that listed in the 2007 Vietnam Red Data Book
Historical, cultural and spiritual structures	Were the national park or national park areas nationally-recognized notable historical, cultural and spiritual sites or structures, yes/no?
Hotels & hostels	Number of beds in accommodation service
Trails	Signposted paths and nature trails in kilometers
Information services	Number of available information services offered (7 in total) (guided walks, botanic garden, museum, tourism service office, environmental education center, center for rescue, creature conservation and development, interpretive/ informative boards)
Tourism cooperation	Number of enterprises contracting/linking the national park for tourism activities offered
Education & research cooperation	Number of domestic and international organizations/institutes that cooperate with the national park in research and educational fields
Diversity of outdoor activities	Number of available recreational activities offered (13 in total) (walking on natural trails, bird watching, spotting wildlife, plant observation, exploring/ visiting caves, climbing/trekking, swimming, camping, campfire, cycling, sailing/boating/kayaking, zipline/canopy tour, fishing)
External access	Distance from the national park to the nearest city of more than 100,000 inhabitants in kilometers: Short (up to 50), Medium (between 50 and 100), and Large (over 100)
Internal assess	Do enterprises contracting/linking to the national park offer internal shuttle services, yes/no?
Local community	Is there a chance to enjoy traditional music/games/cultural activities which will be performed by minorities/local communities when visiting the national park, yes/no?

recreational experience (Findlay and Southwell 2004). Information services, tourism and educational and research cooperation in NPs are also assumed to be important for determining its attractiveness (Dwyer and Kim 2003, Formica and Uysal 2006, Lee et al. 2010) and could create tourism possibilities such as educational tourism in these areas. A variety of recreation activities influence tourists' decisions and their motivation to travel to selected destinations (Formica and Uysal 2006, Saayman and Saayman 2009, Kruger and Saayman 2010, Morrison 2013). The accessibility of the destination (i.e. its internal and external access) may be assessed according to alternative, convenience and distance levels (Deng et al. 2002), which govern the degree of difficulty and convenience of moving from one place to another. Accessibility and transportation is one of the pull factor domains that influence the decisions of tourists to visit protected areas (Kim et al. 2003). Moreover, local communities (e.g. cultural aspect) and peripheral attractions (e.g. importance) are regarded as major elements contributing to the attractiveness of a NP-based tourism destination (Deng et al. 2002, Goodwin 2002).

It is clear from the attribute selection process that protected area-based destinations are complex systems and a range of different attributes may influence the choice

of destination by the tourist, as well as the attractiveness of the destination itself. In this sense, it is necessary to identify the degree to which the selected attributes contribute to the attractiveness of a NP to the tourist in relation to others. Thirteen attributes of a NP (Table 1) were also applied in the selection of Vietnamese NPs for the study.

Data collection

The present study on tourism attractiveness was part of a series of surveys intended for the collection of data related to the management of national parks in Vietnam (*cf.* An et al. 2018). A survey method was used, with a structured questionnaire being sent to the management boards directly responsible for protected area management in 30 Vietnamese NPs (Figure 1). In order to construct the survey questionnaire properly, a mixed-methods approach was undertaken: a review of literature determining the context of protected area management, including tourism activities, was performed (e.g. Puustinen et al. 2009, Lee et al. 2010), followed by discussions with the staff and management boards of the NPs. The survey questionnaire was subsequently pre-tested with six randomly-selected members of management boards. After pre-testing and sub-mitting comments, a structured questionnaire was developed with a total of 26 questions regarding tourism development and management of NPs, among others. After contacting the heads of the management boards in the 30 NPs to explain the purpose of the survey, the questionnaire survey was sent by e-mail between May and December 2016. In addition, the survey was supplemented with phone calls to the respondents to ensure a high rate of response and to gain an insight into the questionnaire. The final response rate to the survey questionnaire was 30/30.

Apart from data survey collection, the study used information collected from secondary data sources (e.g. previous studies and reports) concerning the biodiversity status of protected areas (see Suppl. material 1).

The SMAA and PROMETHEE method

The process of choosing a travel destination can be regarded as a multiple criteria decision analysis problem, whereby destinations are ranked according to the preferences of particular tourists. In such multiple-criteria decision analysis problems (Figueira et al. 2005, Ishizaka and Nemery 2013, Greco et al. 2016), a set of m alternatives

$$A = \{a_1,...,a_i,...,a_m\}$$

is evaluated based on a set of n criteria

$$G = \{g_1,...,g_j,...,g_n\}$$

in order to deal with decision problems such as choosing the best alternative or ranking all alternatives from best to worst. In the case of ranking NP-based tourism attractiveness, the alternatives are Vietnam's national parks (i.e. $m = 30$ NPs) and the criteria are the attributes according to which these parks would be evaluated (i.e. $n = 13$ criteria, see Table 1). Let $g_j(a_i)$ denote the evaluation of alternative a_i on criterion g_j. The final ranking will be achieved by aggregating $g_j(a_i)$ properly to tourist preference. The present study applied the PROMETHEE method for modeling the decision process associated with the ranking performed by each tourist before choosing the final NP destination.

The PROMETHEE method is a well-known outranging method (Hyde et al. 2003), and has been widely applied in various disciplines, including tourism planning (Michailidis and Chatzitheodoridis 2006, Kovačić 2010, Muszyńka-Kurnik 2012, Ranjan et al. 2016). Detailed descriptions of PROMETHEE can be found in Brans and Vincke (1985) and Brans and Mareschal (1994, 2005).

The PROMETHEE method acts by developing a preference function

$$P_j(a, b)$$

which is a function of the difference (d_j) between the ratings of two alternatives

$$(a, b) \in A$$

for each criterion (j), i.e.

$$d_j = g_j(a) - g_j(b)$$

where $g_j(a)$ and $g_j(b)$ are performance values of criterion j of two alternatives a and b, and takes values between 0 and 1. For each criterion, a specific preference function (P_j) must be defined, which can be one of six different functions (Brans and Vincke 1985, Brans and Mareschal (2005), see Appendix 1). In order to compare an alternative a with the other alternatives, the single criterion net flow can be calculated as

$$\phi_j(a) = \frac{1}{n-1} \sum_{x \in A} \left[P_j(a, x) - P_j(x, a) \right]$$

and then the net outranking flow can be calculated as

$$\phi(a) = \sum_{j=1}^{k} \phi_j(a) \, w_j$$

where w_j are weights which describe the importance of each criterion for the decision-maker in case of tourists. The final ranking, also known as a complete PROMETHEE II ranking (Brans and Mareschal 2005), is obtained by comparing net outranking

flows for each alternative. The alternative with the highest net outranking flow is considered the preferred one.

The PROMETHEE method can be used in the case of one decision-maker. In this case, the expressed preferences can be described as the individual weight vector, and the set of parameters of the preference function which correspond with the decision maker's own ranking of alternatives. However, to assess the tourism attractiveness of Vietnamese NPs, it is necessary to not only consider the preferences of a single tourist, but also the preferences of each potential tourist visiting NPs. The best way to achieve this is by the stochastic multicriteria acceptability analysis (SMAA) method.

The SMAA method has been developed for discrete multicriteria problems where criteria values and/or weights or other model parameters are not precisely known (Tervonen and Figueira 2008, Lahdelma and Salminen 2010). A number of SMAA methods are known, such as the original SMAA (Lahdelma et al. 1998), SMAA-2 (Lahdelma and Salminen 2001) or SMAA-PROMETHEE (Corrente et al. 2014), which explore the weight space and describe the valuations that would make each alternative solution the most preferred one, or that would give a certain rank for an alternative.

The decision model in the original SMAA method (Lahdelma et al. 1998) considers multiple decision makers, each with a preference parameter representable through an individual weight vector w and a real-valued partial utility function

$$u(a_i, w) = \sum_{j=1}^{n} w_j g_j(a_i)$$

based on these, a ranking of alternatives is constructed. In case of the SMAA-PROMETHEE method, net outranking flows are used instead of utility functions.

The set of all possible weighting vectors is denoted as feasible weight space and defined as

$$W = \left\{ w \in R^n : w \geq 0, \ \sum_{j=1}^{n} w_j = 1 \right\}$$

In addition, a set of favorable rank weights for alternative i is defined as all possible weight vectors for which alternatives i achieved r rank, defined as

$$W_i^r = \left\{ w \in W : \text{rank}(i, w) = r \right\}$$

where the rank of each alternative is determined as an integer from the best rank (=1) to the worst rank (=m) by means of a ranking function $u(a_i, w)$. The ranking function is defined as

$$\text{rank}(i, w) = 1 + \sum_{k \neq i} p\big(u(a_k, w) > u(a_i, w)\big)$$

where $p(\text{true}) = 1$ and $p(\text{false}) = 0$. Most importantly, the SMAA method outputs descriptive measures such as central weight vectors and rank acceptability indices.

The rank acceptability index can be defined as the ratio between the volume of the set of favorable rank weights and the volume of feasible weight space. This is computed by Monte Carlo simulation as a solution of the multidimensional integral:

$$b_i^r = \int_{w \in W_i^r} f_w(w) \, dw$$

where $f_w(w)$ is a density function of weight distribution. The rank acceptability indices can be interpreted as a percentage of all possible weight vectors which give alternative i rank r within range [0, 1], where 0 indicates that the alternative will never obtain a given rank and 1 indicates that it will always obtain the given rank with any choice of weights. The most acceptable (best) alternatives are those with high acceptability for the best (smallest) ranks. In the present study, rank acceptability indices were used to measure the tourism attractiveness of NPs. More precisely, the rank acceptability index for rank 1

$$b_i^1 = a_i$$

shows how many possible combinations of weights support the first position in the ranking for a particular NP. In other words, it presents the proportion of different decision makers' preferences to schemes, which result in a particular NP being the most attractive.

The central weight vector is the center of gravity for favorable weights space for rank=1. It is computed as an integral of the weight vector over the criteria and weight distributions as

$$w_i^c = \frac{1}{b_i^1} \int_{w \in W_i} f_w(w) \, w \, dw$$

With the assumed weight distribution, the central weight vector is the best single vector representation for a decision-maker who supports alternative i (Lahdelma and Salminen 2001). Decision makers can understand which preferences (criteria weights) lead into which actions, without providing any preference information, by presenting the central weight vectors (Tervonen and Figueira 2008).

Statistical analyses and calculations

In the study, the rank acceptability index is considered as an indicator of tourism attractiveness; however, the problem arises as to which rank acceptability indices should be taken into account. The most obvious solution, i.e. the first rank acceptability index, cannot be implemented in cases where only some alternatives are not being dominated. For the dominated alternatives, regardless of weights, there always exists at least one better alternative, and the first acceptability index is equal 0. However, in practice, dominated NPs are chosen as the final destination by some tourists. In order to avoid this paradox, a model of exponential multiple choices is assumed, where some of the tourists

visit more than one NP, and then choose alternatives from the lower ranks as their next destinations for their sets of weights. In addition, it is assumed that the number of tourists who visit more NPs decreases exponentially with the numbers of visited NPs. In this case, it is possible to construct an exponential weighted acceptability index $b_i^{\exp}$ as

$$b_i^{\exp} \quad = \quad \sum_{r=1}^{n}(1-\lambda)\lambda^{r-1}b_i^r$$

where n is the number of alternatives and r is the rank ($r = 1,\ldots,$n), λ is a parameter of the method and b_i^r is the rank acceptability index for rank r and alternative i. Parameter λ is optimized by a maximization of the Spearman's rank correlation coefficient between exponential weighted acceptability indices and the number of tourists visiting NPs in 2015.

The PROMETHEE method was used to model the ranking process made by each tourist before choosing the destinations. To unify and simplify the model, two types of preference function were applied for the ranking process: usual and linear types. While both types depend on particular criteria, the usual types (Type 1, see Appendix 1) are associated with discrete variables and the linear types (Type 3, see Appendix 1) with continuous variables. For the linear type of general criterion, the threshold of strict preference p has been chosen as a maximum difference between the performance values of alternatives. One exception from this rule has been made for values of tourism cooperation criterion, where the strict preference threshold was set at 25 by expert judgment; this was agreed in response to the overwhelming dominance of Phong Nha - Ke Bang NP and the specification of the criterion for better description of potential preferences. The decision matrix for the tourism performance appraisal of 30 NPs can be found in Appendix 2, and a detailed assumption for NP selection in Appendix 3.

In addition, descriptive measures of SMAA computations are calculated by considering the number of Monte Carlo replications performed in order to obtain a sufficiently accurate approximation (Tervonen and Figueira 2008, Lahdelma and Salminen 2010). For example, an error limit of 0.01 can be accomplished with 95% confidence by performing approximately 10,000 replications (Lahdelma and Salminen 2010). In the present paper, 100,000 replications were generated in order to obtain rank acceptability indices and central weight vectors.

All calculations and statistical analyses in the study were performed using the software package R, version 3.3.3 (R Core Team 2017).

Results

National parks' characteristics

The 30 Vietnamese NPs differ markedly in terms of size, designation, geographical distribution and number of tourists (Table 2). Many NPs or NP areas were also specified under international and regional agreements, including the international designations (Ramsar Site, United Nations Educational, Scientific and Cultural Organisation

Table 2. Vietnamese national parks.

National parks	Year of establishment	Area (ha)	Other designation	Vietnam geographical region	Tourists by years	
					2005	2015
Hoang Lien	2002	28.059	AHP	NW	–	116.305
Ba Be	1992	10.048	RS, AHP	NE	–	45.000
Xuan Son	2002	15.048	–	NE	500	21.780
Cuc Phuong	1962	22.200	–	RRD	63.258	71.600
Cat Ba	1986	17.363	UBR, MPA	RRD	57.000	412.346
Ba Vi	1991	10.815	–	RRD	–	216.050
Tam Dao	1996	34.995	–	RRD	–	14.176
Bai Tu Long	2001	15.783	MPA	RRD	–	12.838
Xuan Thuy	2003	7.100	RS	RRD	3.990	16.482
Bach Ma	1991	37.487	–	NCC	8.926	14.852
Ben En	1992	14.735	–	NCC	–	9.892
Pu Mat	1997	91.113	UBR	NCC	7.837	4.186
Phong Nha – Ke Bang	2001	123.326	UWHS	NCC	255.923	714.835
Vu Quang[*]	2002	57.038	UBR	NCC	–	–
Cat Tien	1992	72.634	UBR, RS	CH	16.043	26.664
Yok Don	1992	115.545	–	CH	–	1.760
Chu Mom Ray[*]	2002	56.621	AHP	CH	–	–
Kon Ka Kinh[*]	2002	42.143	AHP	CH	–	–
Chu Yang Sin	2002	58.971	–	CH	–	30.000
Bidoup-Nui Ba	2004	70.038	UBR	CH	–	7.442
Nui Chua	2003	29.865	MPA	SCC	–	530
Phuoc Binh	2006	19.814	–	SCC	–	1.200
Con Dao	1993	20.000	RS, MPA	SE	–	19.753
Bu Gia Map	2002	25.779	–	SE	–	1.239
Lo Go – Xa Mat	2002	19.156	–	SE	–	3.369
Tram Chim	1998	7.588	RS	MRD	–	175.208
Phu Quoc[*]	2001	29.421	UBR, MPA	MRD	–	–
U Minh Thuong	2002	8.038	UBR, RS, AHP	MRD	–	50.040
Mui Ca Mau	2003	41.862	UBR, RS	MRD	–	109.372
U Minh Ha	2006	8.528	UBR	MRD	–	16.886

List of abbreviations: UWHS: United Nations Educational, Scientific and Cultural Organisation World Heritage Site; UBR: United Nations Educational, Scientific and Cultural Organisation Biosphere Reserve; RS: Ramsar Site; AHP: Association for Southeast Asian Nations Heritage Park; MPA: Marine Protected Area. NW: North West; NE: North East; RRD: Red River Delta; NCC: North Central Coast; CH: Central Highlands; SCC: South Central Coast; SE: South East; MRD: Mekong River Delta
[*]At the time of the study, visitor statistics were not available; – Lack of data

[UNESCO] World Natural Heritage Site and UNESCO Biosphere Reserve), as well as regional designations including the Association for Southeast Asia Nations Heritage Parks. Some NPs were listed in the system of Marine Protected Areas.

In the context of tourism development, the majority of NPs (87%) administered tourism activities (Table 2), which generated a significant source of funds for protected areas. Over the past decade, the total number of tourists visiting NPs has risen even more steeply, i.e. by over 500%, reaching 2,113,805 in 2015. It was found that Phong Nha – Ke Bang NP attracted the highest number of tourists in 2015, with a total of 714,835 tourists.

Ranking of tourism performance of Vietnamese national parks

The obtained rank acceptability indices, calculated according to the SMAA-PRO-METHEE method, for 30 Vietnamese NPs are presented in Table 3 (see Suppl. material 2). It was found that Phong Nha - Ke Bang NP is the most attractive of all tested parks in Vietnam over the widest range of preference structure. Phong Nha – Ke Bang NP has about 70% of possible preference structures, making it the most preferred. The second and third most attractive NPs were found to be Cuc Phuong and Ba Be, with 20% and 6% of possible weight structures respectively. In total, Phong Nha - Ke Bang, Cuc Phuong and Ba Be NPs appear to be the most attractive to tourists, with more than 95% of all possible preference structures. In addition to the results, 18 NPs were dominated by the other 12 NPs (Table 3). Hence, there would be always at least one NP which is more interesting regarding tourism attractiveness, regardless of tourist preference structure.

Since 18 NPs were dominated (Table 3), they have no central weight vectors. For the remaining 12 NPs (i.e. non-dominated NPs), central weight vectors can be calculated (Appendix 4). A graphical representation of central weight vectors (Figure 2 and Appendix 4) as well as the importance of each criterion among all other criteria (Table 4 and Appendix 4) clearly describe the average preferences of a particular NP visitor. In particular, the criterion of trails was the most, or almost one of the most, important criteria for supporters of all non-dominated NPs, except for Cat Tien and Phong Nha – Ke Bang NPs.

Spearman's rank correlation coefficient was employed to assess the correlation between tourism attractiveness and the number of tourists who visited the NPs. The comparison was carried out for only 26 NPs due to a lack of data on the number of tourists of four NPs (Table 2). The maximum achieved Spearman's rank correlation coefficient between the number of tourists and exponential weighted acceptability index was 0.285 (p = 0.173) for λ between 0.137 and 0.146. In other words, 13 criteria taken into consideration were able to describe the tourist attractiveness of NPs with 28.5% probability, and it was found to be statistically significant at the p=0.05 level. The low value of λ (0.137) indicates that the proportion of tourists visiting only a single NP is around 85%.

Discussion

National parks in Vietnam are an essential part of the national development strategy for the countryside, as well as nature protection (PARC Project 2006). Hence, effective planning and management of tourism in NPs is crucial in order to ensure sustainable conservation of natural resources, achievement of long-term objectives of protected area management, and ready adaptation to national, regional and local development plans (Eagles et al. 2001, 2002). It is also essential to consider the characteristics of NBT destinations when supporting the management plans of protected areas (Puustinen et al. 2009).

Table 3. Rank acceptability indices for Vietnamese national parks.

National Park	Rank acceptability index for rank (%)					Sum of rank acceptability indices for ranks (%)		
	1	**2**	**3**	**4**	**5**	**6–10**	**11–20**	**21–30**
Phong Nha - Ke Bang[*]	70.423	14.702	6.944	3.004	1.767	2.723	0.437	0.000
Cuc Phuong[*]	20.324	31.976	20.639	11.963	6.431	8.451	0.216	0.000
Ba Be[*]	5.462	28.521	28.774	17.852	9.651	9.598	0.142	0.000
Hoang Lien[*]	1.234	9.995	13.454	15.471	16.155	40.133	3.556	0.002
Bidoup-Nui Ba[*]	1.077	2.891	4.755	7.751	12.613	64.718	6.195	0.000
Tam Dao[*]	0.839	1.990	3.269	6.418	9.663	65.159	12.558	0.104
Cat Ba[*]	0.609	3.877	5.521	9.399	11.800	59.309	9.485	0.000
Cat Tien[*]	0.091	5.051	13.072	20.088	15.629	38.939	7.127	0.003
Nui Chua[*]	0.005	0.038	0.124	0.335	0.550	26.944	70.294	1.710
Chu Yang Sin[*]	0.002	0.006	0.008	0.023	0.052	2.558	63.348	34.003
Ba Vi[*]	0.001	0.958	3.015	6.510	12.676	69.963	6.869	0.008
Pu Mat[*]	0.001	0.046	0.410	1.100	2.655	54.713	39.827	1.248
Bach Ma	0.000	0.000	0.001	0.003	0.005	13.794	85.111	1.086
Bai Tu Long	0.000	0.000	0.000	0.000	0.001	0.672	51.102	48.225
Ben En	0.000	0.000	0.000	0.000	0.008	9.162	84.733	6.097
Bu Gia Map	0.000	0.000	0.005	0.030	0.189	12.980	82.180	4.616
Chu Mom Ray	0.000	0.000	0.000	0.000	0.000	0.000	0.082	99.918
Con Dao	0.000	0.000	0.000	0.000	0.000	0.000	9.928	90.072
Kon Ka Kinh	0.000	0.000	0.000	0.000	0.000	0.000	0.865	99.135
Lo Go - Xa Mat	0.000	0.001	0.005	0.005	0.013	1.321	59.968	38.687
Mui Ca Mau	0.000	0.000	0.000	0.000	0.001	0.442	16.413	83.144
Phu Quoc	0.000	0.000	0.000	0.000	0.000	0.142	22.698	77.160
Phuoc Binh	0.000	0.000	0.000	0.001	0.002	1.992	70.258	27.747
Tram Chim	0.000	0.000	0.000	0.002	0.002	1.324	56.475	42.197
U Minh Ha	0.000	0.000	0.000	0.000	0.000	0.014	3.653	96.333
U Minh Thuong	0.000	0.000	0.000	0.000	0.000	0.321	49.391	50.288
Vu Quang	0.000	0.000	0.000	0.001	0.002	0.260	24.251	75.486
Xuan Son	0.000	0.000	0.000	0.000	0.000	0.000	3.279	96.721
Xuan Thuy	0.000	0.000	0.004	0.042	0.118	11.576	77.054	11.206
Yok Don	0.000	0.000	0.000	0.000	0.003	2.734	82.545	14.718

[*] National parks were not dominated

The present study explores some of the attributes and characteristics of NPs associated with the initial evaluation of tourism attractiveness and destinations in 30 Vietnamese NPs. The findings not only contribute to a deeper understanding of the managerial context of NPs, but also provide information on the performance appraisal of NPs with regard to tourism. The study highlights the relative importance of attributes with regard to the tourism attractiveness of NP-based destinations and orders them into a ranking system.

The ranking of the national parks by the SMAA and PROMETHEE model suggests a degree of competition exists regarding the tourism attractiveness and tourism performance of protected areas. Our present findings indicate that Phong Nha - Ke Bang NP has the most competitive position. Phong Nha - Ke Bang is situated in Central Vietnam, 40km north of Dong Hoi City (Quang Binh Province) and 500km south of Ha Noi City, and possesses outstanding historical and cultural resources such as cave systems and indig-

Table 4. The importance of criteria supporting particular national parks. The heat map represents the average proportional relative importance of each criterion to a national park supporter, with the scale ranging from green (the least important) to red (the most important).

National park	IN	BD	RR	HS	HH	IS	TR	TC	EC	DA	EA	IA	LC
Phong Nha – Ke Bang	2	10	4	7	11	12	13	5	3	6	1	9	8
Cuc Phuong	13	4	11	7	3	2	1	5	10	9	12	6	8
Ba Be	2	11	5	6	4	1	3	13	9	10	12	8	7
Hoang Lien	11	4	6	7	12	9	1	8	3	10	2	13	5
Bidoup-Nui Ba	2	8	10	13	9	12	1	6	7	11	3	5	4
Tam Dao	11	9	6	4	8	3	1	10	13	7	2	5	12
Cat Ba	4	10	11	6	7	8	1	13	9	2	3	5	12
Cat Tien	2	8	12	13	9	1	11	7	3	5	10	4	4
Nui Chua	10	8	12	8	6	5	1	11	7	13	2	3	4
Chu Yang Sin	9	11	2	3	9	13	1	7	6	5	11	8	4
Ba Vi	10	8	10	6	7	10	2	8	1	4	5	2	10
Pu Mat	1	4	12	5	7	3	2	6	10	7	7	12	10

List of abbreviations: IN: International importance; BD: Biodiversity of plants and animals; RR: Rare plants and animals; HS: Historical, cultural and spiritual structures; HH: Hotels & hostels; IS: Information services; TR: Trails; TC: Tourism cooperation; EC: Education & research cooperation; DA: Diversity of outdoor activities; EA: External access; IA: Internal access; LC: Local community.

enous groups (UNESCO 2014). Phong Nha - Ke Bang NP dominates other NPs: it had the highest acceptability index (70%) for the best rank, fairly high acceptability for the second and third ranks, and almost zero acceptability for ranks four to thirty (Table 3).

The competitiveness of NPs in Vietnam appears uneven: while the three best NPs (Phong Nha – Ke Bang, Cuc Phuong, and Ba Be) were the most attractive for 95% of potential tourists, 60% of NPs were dominated by the best NPs and were not able to compete effectively with them. According to the Vietnam tourism master plan until 2020 (GoV 2013), over half of the 12 identified non-dominated NPs (e.g. Phong Nha - Ke Bang, Cuc Phuong, Ba Be, Hoang Lien, Cat Tien, Tam Dao, Ba Vi) were considered tourist sites (zones) and were prioritized by investment projects for the development of national tourism. It is also important to consider these 12 NPs when developing nature-based tourism strategies or plans at regional and national levels.

It was found that each criterion (attribute) contributed a different value towards the attractiveness of the 12 non-dominated NPs (Figure 2, Tables 3, 4). The results are in line with those of Deng et al. (2002) and Lee et al. (2010), who found that selected criteria did not contribute equally to the weights determining attractiveness. The obtained central weights reveal the preferences of a potential tourist who visits a certain NP, and indicate the advantages and disadvantages of all 12 NPs (Figure 2, Table 4). Contrary to Deng et al. (2002), natural characteristics, such as biodiversity or rare species of animals and plants, were not considered to be the most important criteria supporting the attractiveness of a particular NP for tourists, which suggests that it is necessary to consider the knowledge and perspectives of both experts and tourists when making a decision. However, there is currently no shared biodiversity database or any biodiversity monitoring system applied to protected areas. These deficiencies constitute one of multiple
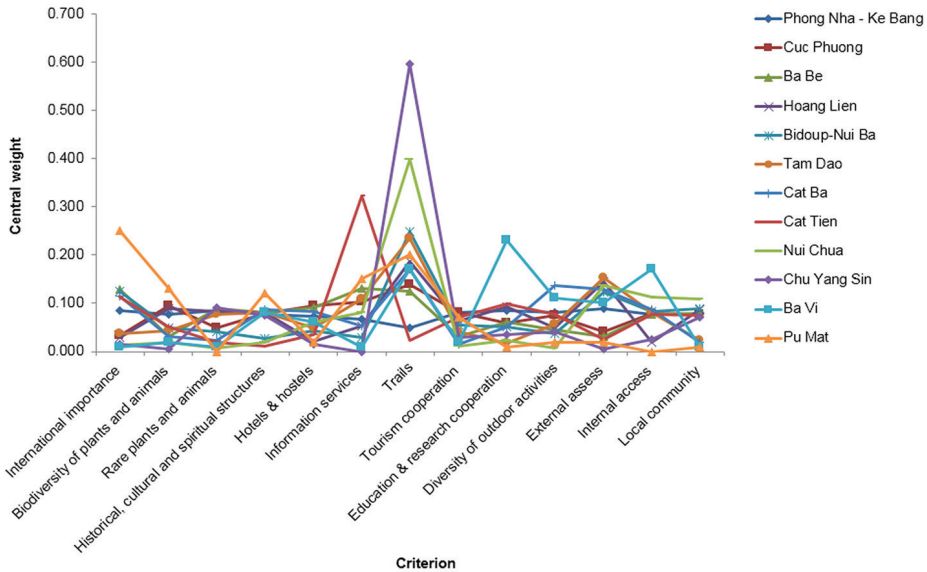
Figure 2. Central weight vectors of national parks.

challenges faced by decision makers regarding the sustainable development of natural resources and effective protected area management in Vietnam (MONRE 2011, 2014). Increasing the amount of available information regarding the updated biodiversity status of protected areas could improve the tourism attractiveness of particular NPs such as Ba Vi and Nui Chua (Table 4). In particular, NPs should highlight their unique and rare natural assets, such as flagship and iconic species, in order to distinguish them from other NP-based destinations. Even highlighting the engagement of organizations in conservation initiatives could become a valuable part of marketing activities for species and nature-based tourism experiences in protected areas (Ballantyne et al. 2009).

The trail criterion identified in the present findings plays a crucial role for supporters of most non-dominated parks; hence the trail attribute appears to be the most important of the recreation facilities affecting forest-based tourism attractiveness (Lee et al. 2010). As recreational facilities within NPs, trails are an attraction for both casual and serous hikers and may take tourists into a range of areas, such as natural ecosystems and the primitive interior of protected areas (Manning and Anderson 2012), and provide opportunities for a variety of outdoor recreation activities, such as walking and hiking. The high importance of the trail criterion was also connected with the fact that it is a weak point of Phong Nha - Ke Bang. In this sense, tourists who are attracted by long-distance trails are more likely to prefer other NPs, such as Chu Yang Sin NP (Figure 2, Table 4). NP managers should consider designing, developing and planning recreational trail networks for tourists that could help them appreciate natural resources or most attractive parts of NPs, provide and operate health enhancement facilities, and offer various levels and durations of experience (Eagles et al. 2001, 2002, Kim et al. 2003).

Moreover, it was found that other criteria with discriminating power were its international importance -this being the most important criterion for Pu Mat. Information services was a significant criterion for Ba Be, Cat Tien and Cuc Phuong. Education and research cooperation was the most important criterion for Ba Vi, and external access was the important criterion for Phong Nha - Ke Bang, Hoang Lien, Tam Dao and Nui Chua (Table 4). As one of the labels, or intangible elements, the international importance of an NP or NP areas is regarded as playing an important role in increasing its attractiveness and its successful marketing (Palmer 1999); for example, recognition as a UNESCO World Heritage site is believed to draw millions of tourists to these sites (Yan and Morrison 2008). To attract tourists, NP managers (i.e. marketers) of internationally recognized sites should promote them as such in the mass media and guidebooks, and compare them with other NPs, e.g. Phong Nha - Ke Bang is the only NP under the UNESCO World Heritage List (see Table 2). The development of information services in NPs reflect partly the investment in the tourism infrastructure of a destination, but also contribute toward improving destination repositioning and may significantly increase tourist flows to protected areas (Puustinen et al. 2009, Castro et al. 2015). Extending education and research cooperation with domestic schools and universities also encourages the growth of educational tourism in Vietnam's NPs; for example, by organizing educational tourism activities for students. Many of the domestic tourists visiting protected areas are students on school or university outings, and there is great potential for developing environmental education activities for them (ICEM 2003). Tourism cooperation, as one of the key components of the nature tourism industry, encourages tourists to visit destinations and promotes more positive images of destinations (Higgins 1996, Carey et al. 1997, Cavlek 2002, Dwyer and Kim 2003). The degree of external access to protected areas is influenced by the state of the public transportation infrastructure and multimodal transport in the region. Tourists will seek alternative destinations if accessibility to a preferred tourism destination is limited, for example by comfort levels and journey time in the transport system (Prideaux 2000).

Our present findings also suggest that the development of NP-based tourism destinations in Vietnam is uneven. In particular, the development of tourism in protected areas, where most NPs suffer from a lack of services and facilities for tourism, is faced by multiple challenges; several NPs are characterised by logging and unavailable trails (see Appendix 2). The issues are similar to those identified by the PARC Project (2006), which found that more than 60% of the state budget of the Vietnamese Government for protected areas went to infrastructure development. On the other hand, most NPs spent about half of their funds on conservation activities, and financial allocations for protected area management could also change over time (An et al. 2018). In this context, considering the allocation of financial sources and investment in tourism, particularly in tourism infrastructure, would be an effective contribution to the management of tourism in NPs. This would also help NP managers create a sound investment plan for their priority actions, such as trails/recreational facilities.

The tourism attractiveness of a NP, i.e. its attractiveness to tourists, significantly correlated with the number of tourists visiting it. This was consistent with the result for

Phong Nha - Ke Bang NP, which was rated as the most attractive park and attracted the highest number of tourists in 2015 (Table 2). However, despite receiving a high number of tourists, some protected areas such as Mui Ca Mau, Tram Chim and U Minh Thuong NPs were assigned low acceptability indices to higher ranks, as low competitive strengths; for example, with a high number of 109,372 tourists in 2015, Mui Ca Mau had the highest acceptability (83%) for the 21–30 rank (Tables 2, 3). Hence, only about 29% of the criteria in the model explained the level of tourism attractiveness with respect to the tourist numbers. In other words, apart from 13 selected criteria in the study, NP tourism attractiveness could be predicted through other criteria, such as population density and tourist services outside the NP (Puustinen et al. 2009, Castro et al. 2015). Contrary to Mui Ca Mau NP, Bidoup-Nui Ba was found to be an attractive destination, but only about 7,500 tourists visited the park in 2015 (Tables 2, 3). This suggests that Bidoup-Nui Ba managers should promote marketing activities to highlight their potential advantages (i.e. trails, external access, international importance, and local community) and attract more tourists.

In addition to its methodological qualities, the results indicate that integrating the SMAA and PROMETHEE methods could serve as a useful approach for supporting decision making when ranking NP-based tourism destinations, and provide decision makers with information for determining the position of a destination. However, it may not be realistic to develop a decision model that fits all decision makers and every decision situation (Sirakaya and Woodside 2005). Although the main purpose of a NP is to protect nature and provide recreation possibilities, each NP has different objectives for natural resource management and tourism development. In this context, further research regarding the various aspects of decision making is necessary when making trade-offs between nature protection and tourism development in protected area management. Such trade-offs and conflicts between stakeholders are common, and the conservation of species and habitats and other natural values and the intensity in both of them tend to increase when a protected area-based destination becomes more attractive to tourists. For example, the most common basic sources of tension appear to occur between operators seeking greater and closer access to wildlife and the protected area managers seeking to restrict access and increase the distance between visitors and species (Reynolds and Braithwaite 2001). The conflict between the need to protect the ecological integrity of an area and to provide facilities for visitors requires careful management and long-term monitoring of tourist impact (Goodwin 1996). Moreover, trade-off analysis could bring together diverse quantitative and qualitative information for decision making, thus allowing tourism development options to be ranked on the basis of different stakeholder values (Brown et al. 2001).

In trying to evaluate the attractiveness and the performance of 30 Vietnamese NPs in the context of NBT management, the present study was limited to criteria that are easily measured. Other attributes of a protected area, such as image, climatic phenomena, landscapes and scenery, can be assumed to affect the tourism attractiveness and destination choice (Dwyer and Kim 2003, Hsu et al. 2009, Lee et al. 2010), but were not included in the present analysis. Even Lee et al. 2010 found that the uniqueness

of forest landscapes and scenery and special climate phenomena are two of the most important attributes determining the attractiveness of forest-based tourism. In this sense, the beautiful scenic mountain landscapes of many Vietnamese NPs situated in relatively remote areas may have an influence over their tourism attractiveness and their tourist flows. The aesthetic of a tourism destination should also be considered when evaluating the tourist experience, as it has been found to be the most important factor for tourists (Dodds et al. 2010). In other words, a variety of diagnostic attributes that may affect the attractiveness of a NP directly and indirectly, as well as the implementation of tourism should be appraised for further study.

Furthermore, the present study lacks the perspective of decision makers or different stakeholders; for example, domestic and foreign tourists who not only directly use the natural resources of a NP but also can evaluate its attributes as a destination (Michailidis and Chatzitheodoridis 2006, Hsu et al. 2009). It is important to consider expert opinions when determining attributes and their relative importance (Lee et al. 2010), particularly in the context of managing the natural resources of protected areas, and their values and assets which could be essential when performing multi-criteria analyses and evaluating NP-based tourism destinations. In addition, the study does not examine perceptions or attitudes of tour operators and travel agencies; tour operators have considerable influence on the choice of travellers, tourism strategies, and the development plans of tourism destinations (Carey et al. 1997, Sigala 2008).

These approaches raise some key questions, e.g. how to use potential NP attributes to attract tourists, how to determine the attractiveness of NP-based tourism, how to involve stakeholders and evaluate their role in the tourism management of NPs, how NBT can be developed while maintaining a high level of ecosystem and biodiversity. Although the precise answers to these questions remain unclear, the approach taken in the present study is an effective method of evaluating the characteristics of NPs and their tourism performance. Such evaluation represents a crucial step in addressing these questions, as well as in improving the effective management of protected areas. Taking this approach will allow more effective planning and development of protected area-based tourism and sustainable tourism in Vietnam.

Conclusion

SMAA and PROMETHEE have been widely applied to deal with various real-world problems (Hyde et al. 2003, Brans and Mareschal 2005, Tervonen and Figueira 2008). The present study used an integration of SMAA and PROMETHEE methods, and it proposed a new index (i.e. the exponential weighted acceptability index) for the measurement of NP tourism attractiveness. Our findings indicate that Phong Nha - Ke Bang, Cuc Phuong and Ba Be NPs gave the best performance of 30 studied national parks in Vietnam, with respect to tourism attractiveness. In addition, 12 NPs were found to be non-dominated, and the trail criterion appears to be the most important central weight vector supporting most of these parks. A statistically significant correlation was also

found between the tourism attractiveness of a national park and the number of tourists visiting it. However, improving tourism attractiveness should not only aim at increasing tourist flows to a national park. It should also facilitate the development of sustainable nature-based tourism and the main objectives of national parks. Further studies can build upon the present findings to obtain more precise strategies for fostering NP-based tourism in order to improve the effectiveness of management of national parks, and promote sustainable development of NBT in protected areas in Vietnam.

Acknowledgments

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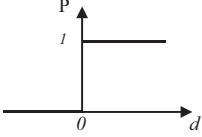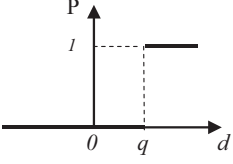Kim D, Perdue RR (2011) The influence of image on destination attractiveness. Journal of Travel & Tourism Marketing 28(3): 225–239. https://doi.org/10.1080/10548408.2011.562850
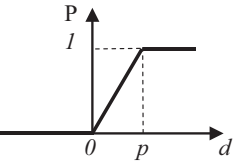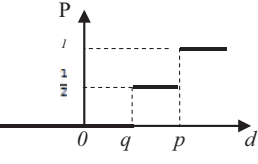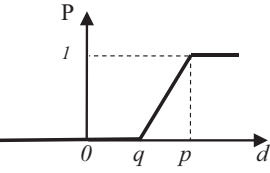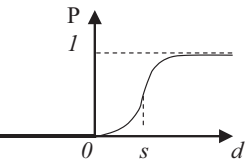
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Appendix I

Types of generalized criteria and their corresponding preference functions. Source: Adapted to Brans and Mareschal (2005).

Name of the Criterion	Preference function	Parameters
Type 1: Usual Criterion	$P(d) = \begin{cases} 0 & d \leq 0 \\ 1 & d > 0 \end{cases}$	None
Type 2: U-shape Criterion	$P(d) = \begin{cases} 0 & d \leq q \\ 1 & d > q \end{cases}$	q
Type 3: V-shape Criterion with linear preference	$P(d) = \begin{cases} 0 & d \leq 0 \\ \dfrac{d}{p} & 0 \leq d \leq p \\ 1 & d > p \end{cases}$	p
Type 4: Level Criterion	$P(d) = \begin{cases} 0 & d \leq q \\ \dfrac{1}{2} & q \leq d \leq p \\ 1 & d > p \end{cases}$	p, q
Type 5: V-shape Criterion with indifference and linear preference	$P(d) = \begin{cases} 0 & d \leq q \\ \dfrac{d - q}{p - q} & q < d \leq p \\ 1 & d > p \end{cases}$	p, q
Type 6: Gaussian Criterion	$P(d) = \begin{cases} 0 & d \leq 0 \\ 1 - e^{-\frac{d^2}{2s^2}} & d > 0 \end{cases}$	s

Appendix 2

Decision matrix for the tourism performance appraisal of Vietnamese national parks. List of abbreviations: IN: International importance; BD: Biodiversity of plants and animals; RR: Rare plants and animals; HS: Historical, cultural and spiritual structures; HH: Hotels & hostels; IS: Information services; TR: Trails; TC: Tourism cooperation; EC: Education & research cooperation; DA: Diversity of outdoor activities; EA: External assess; IA: Internal access; LC: Local community.

National park	Criteria												
	IN[*]	BD[**]	RR[**]	HS[*]	HH[*]	IS[*]	TR[*]	TC[*]	EC[*]	DA[*]	EA[*]	IA[*]	LC[*]
Ba Be	1	2536	153	1	300	7	9	5	9	7	2	1	1
Ba Vi	0	3075	137	1	160	4	6	5	10	9	3	1	0
Bach Ma	0	3669	148	1	44	4	7.7	1	5	5	2	1	0
Bai Tu Long	0	1111	108	0	0	7	0	0	4	5	3	1	0
Ben En	0	2734	94	1	160	6	5	0	2	6	3	0	0
Bidoup-Nui Ba	1	2680	109	0	60	4	41.1	8	6	6	3	1	1
Bu Gia Map	0	1874	97	1	48	5	39.5	0	5	5	1	1	1
Cat Ba	1	2329	94	1	256	6	24.3	0	7	11	3	1	0
Cat Tien	1	3139	117	0	130	7	0	28	12	9	2	1	1
Chu Mom Ray	0	2142	81	0	0	3	0	0	0	2	2	0	0
Chu Yang Sin	0	1402	106	1	0	2	78	1	0	6	2	0	1
Con Dao	0	1212	28	0	48	4	8.4	1	3	6	1	0	0
Cuc Phuong	0	4510	125	1	380	7	35	50	8	9	2	1	1
Hoang Lien	0	3795	150	1	40	6	27	26	10	7	3	0	1
Kon Ka Kinh	0	1578	69	0	0	3	0	0	1	1	3	0	0
Lo Go - Xa Mat	0	1236	35	1	20	4	60	0	3	6	3	0	0
Mui Ca Mau	1	439	28	1	0	2	0	0	0	7	1	0	1
Nui Chua	0	1834	76	0	60	5	46	7	3	4	3	1	1
Phong Nha – Ke Bang	1	3774	195	1	170	6	0	300	13	10	3	1	1
Phu Quoc	1	1561	65	1	0	0	0	0	7	6	1	0	0
Phuoc Binh	0	1552	86	0	50	2	3	10	4	4	3	0	1
Pu Mat	1	3764	150	1	72	7	15	2	5	5	1	0	0
Tam Dao	0	2581	148	1	120	7	44	5	0	7	3	1	0
Tram Chim	1	545	52	0	24	2	0	2	4	6	3	1	0
U Minh Ha	1	374	28	0	30	2	0	0	3	4	3	0	0
U Minh Thuong	1	682	40	0	20	3	5	3	5	5	2	1	0
Vu Quang	1	2508	184	0	0	1	0	0	4	3	2	0	0
Xuan Son	0	2226	117	0	0	4	0	0	0	3	2	0	0
Xuan Thuy	1	756	11	1	30	5	0	15	9	5	2	1	0
Yok Don	0	1388	80	0	42	6	39	5	0	5	2	1	1

Sources: [*]Survey data (2016); [**]Suppl. material 1

Appendix 3

Assumptions for national park selection.

Criteria	Value	Preference function	q	p	Max/Min
International designation	1 = Yes, 0 = No	Usual	0	1	Max
Biodiversity of plants and animals	Numeric variables	Linear	0	4136	Max
Rare plants and animals	Numeric variables	Linear	0	184	Max
Historical, cultural and spiritual structures	1 = Yes, 0 = No	Usual	0	1	Max
Hotels & hostels	Numeric variables	Linear	0	380	Max
Information services	Numeric variables	Linear	0	7	Max
Trails	Numeric variables	Linear	0	78	Max
Tourism cooperation	Numeric variables	Linear	0	25	Max
Education & research cooperation	Numeric variables	Linear	0	13	Max
Diversity of outdoor activities	Numeric variables	Linear	0	10	Max
External access	3 = Short, 2 = Medium, 1 = Large	Level	0	1	Max
Internal assess	1 = Yes, 0 = No	Usual	0	1	Max
Local community	1 = Yes, 0 = No	Usual	0	1	Max

Appendix 4

Central weight vectors. List of abbreviations: IN: International importance; BD: Biodiversity of plants and animals; RR: Rare plants and animals; HS: Historical, cultural and spiritual structures; HH: Hotels & hostels; IS: Information services; TR: Trails; TC: Tourism cooperation; EC: Education & research cooperation; DA: Diversity of outdoor activities; EA: External assess; IA: Internal access; LC: Local community.

National park	IN	BD	RR	HS	HH	IS	TR	TC	EC	DA	EA	IA	LC
Phong Nha – Ke Bang	0.085	0.077	0.084	0.077	0.073	0.066	0.048	0.081	0.085	0.081	0.088	0.077	0.077
Cuc Phuong	0.034	0.094	0.049	0.078	0.095	0.103	0.139	0.080	0.058	0.074	0.041	0.079	0.077
Ba Be	0.128	0.032	0.089	0.081	0.090	0.131	0.125	0.032	0.060	0.044	0.032	0.077	0.079
Hoang Lien	0.029	0.088	0.083	0.081	0.022	0.053	0.187	0.063	0.093	0.048	0.145	0.020	0.087
Bidoup–Nui Ba	0.125	0.049	0.041	0.027	0.042	0.030	0.249	0.055	0.050	0.038	0.123	0.083	0.089
Tam Dao	0.037	0.043	0.077	0.081	0.048	0.108	0.235	0.040	0.018	0.056	0.152	0.081	0.024
Cat Ba	0.115	0.031	0.023	0.086	0.083	0.053	0.170	0.016	0.050	0.136	0.128	0.087	0.020
Cat Tien	0.112	0.050	0.019	0.012	0.036	0.323	0.024	0.070	0.098	0.076	0.026	0.077	0.075
Nui Chua	0.014	0.020	0.008	0.020	0.060	0.080	0.398	0.012	0.024	0.008	0.136	0.112	0.108
Chu Yang Sin	0.015	0.005	0.090	0.075	0.015	0.000	0.595	0.030	0.035	0.040	0.005	0.025	0.070
Ba Vi	0.010	0.020	0.010	0.080	0.060	0.010	0.170	0.020	0.230	0.110	0.100	0.170	0.010
Pu Mat	0.250	0.130	0.000	0.120	0.020	0.150	0.200	0.070	0.010	0.020	0.020	0.000	0.010

Supplementary material 1

Biodiversity in Vietnam's national parks

Authors: Le Thanh An, Janusz Markowski, Maciej Bartos, Agnieszka Rzenca, Piotr Namiecinski

Data type: species data

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/natureconservation.32.30753.suppl1

Supplementary material 2

Rank acceptability indices for 30 national parks in Vietnam

Authors: Le Thanh An, Janusz Markowski, Maciej Bartos, Agnieszka Rzenca, Piotr Namiecinski

Data type: species data

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/natureconservation.32.30753.suppl2

RESEARCH ARTICLE

The role of herbivorous insects and pathogens in the regeneration dynamics of *Guazuma ulmifolia* in Panama

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Abstract

A significant proportion of the mortality of rainforest trees occurs during early life stages (seeds and seedlings), but mortality agents are often elusive. Our study investigated the role of herbivorous insects and pathogens in the early regeneration dynamics of *Guazuma ulmifolia* (Malvaceae), an important tree species in agroforestry in Central America. We reared pre-dispersal insect seed predators from *G. ulmifolia* seeds in Panama. We also carried out an experiment, controlling insects and pathogens using insecticide and/or fungicide treatments, as well as seed density, and compared survivorship of *G. ulmifolia* seeds and seedlings among treatments and relative to untreated control plots. We observed (1) high pre-dispersal

attack (92%) of the fruits of *G. ulmifolia*, mostly by anobiine and bruchine beetles; (2) negligible post-dispersal attack of isolated seeds by insects and pathogens; (3) slow growth and high mortality (> 95%) of seedlings after 14 weeks; (4) low insect damage on seedlings; and (5) a strong positive correlation between seedling mortality and rainfall. We conclude that for *G. ulmifolia* at our study site the pre-dispersal seed stage is by far the most sensitive stage to insects and that their influence on seedling mortality appears to be slight as compared to that of inclement weather. Thus, the regeneration of this important tree species may depend on effective primary dispersal of seeds by vertebrates (before most of the seed crop is lost to insects), conditioned by suitable conditions in which the seedlings can grow.

Keywords

Anobiidae, fungal pathogen, negative density-dependence, rainforest, seed predation

Introduction

In tropical rainforests a significant proportion of tree mortality occurs during the early life stages of the plant (seeds and seedlings), and patterns of mortality at these early stages of life may be critical in influencing the diversity of older individuals (Massad 2013; Green et al. 2014). There is growing evidence that interactions between plants and host-specific insect herbivores and pathogens could be a central mechanism for explaining plant diversity (Leigh et al. 2004). A mechanism proposed to facilitate the coexistence of tree species in tropical forests is negative density-dependence or the so-called Janzen-Connell effect (Janzen 1970; Connell 1971; Bell et al. 2006; Comita et al. 2010; Bagchi et al. 2014). Seeds are most likely to disperse to sites near their parent trees, but seeds and seedlings are also more likely to survive away from parents where they are less likely to be attacked by host-specific insects and pathogens, which may disperse contagiously from parent trees. Negative density-dependence is the result of the proliferation of species-specific herbivores and pathogens among hosts in areas of high conspecific plant densities, and the negative correlation between enemy propagation and the distance from parent trees to their nearby offspring (Janzen 1970; Connell 1971; Bell et al. 2006; Comita et al. 2010; Bagchi et al. 2014).

Insects, more than herbivorous mammals, are responsible for most herbivory on seedlings in tropical rainforests (Cruz and Dirzo 1987). In addition, many insects, but very few mammals, preferentially attack seeds or plants near conspecific adults (Hammond and Brown 1998). While there have been many studies assessing insect herbivory (foliar damage) and resulting seedling mortality (review in Massad 2013), community studies targeting the insects feeding on rainforest seedlings are relatively rare (Basset 1999; Alvarez-Loayza and Terborgh 2011). Ecologists often infer the impact of insect herbivores on plants by measuring the apparent, or rate of, leaf damage (Coley 1983; review in Lowman 1984), because of the relatively low density of herbivores in tropical rainforests (Novotny and Basset 2000). However, such studies are known to underestimate the magnitude and impact of herbivory significantly because herbivores may eat whole leaves, or disproportionately damage buds and young or expanding leaves (Lowman 1984). This issue may be critical during the seed-to-seedling transition (germinating seed or very young seedling). Although damage by sap-sucking insects on

seeds or seedlings may be difficult to quantify, it may nevertheless lower plant fitness significantly via direct action or the spreading of diseases (Nault and Ammar 1989).

Seedling establishment and survival in tropical rainforests may also be influenced by pathogens, especially fungal pathogens (Augspurger 1984; Mangan et al. 2010; Bagchi et al. 2014). For example, Augspurger (1984) reported that on Barro Colorado Island in Panama, dependent on the tree species, 2–74% of seedlings may be dead from disease two months after germination. Disease incidence is often host-density dependent and may have the potential to regulate host spatial distribution (Augspurger 1984). Further, interactions between herbivory and fungal pathogens may in some cases be significant and affected by anthropogenic disturbance.

One way to assess the effect of insect herbivores or fungal pathogens on rainforest seeds or seedlings is to exclude them with (a) insecticide and/or fungicide or (b) mesh exclosures in treatment plots and compare survivorship of seeds or seedlings between treatment plots and control plots (Swamy and Terborgh 2010; Bagchi et al. 2014). Bagchi et al. (2014) used method (a) to study the role of insects and fungal pathogens in causing mortality to seeds and young seedlings in a rainforest in Belize. They found that spraying insecticides on seeds and germinating seedlings increased overall seedling survival dramatically (by a factor of 2.7). The benefits of insecticide application varied among plant species, so that excluding insects changed the structure of the seedling community considerably. These initial results suggest that insects and pathogens play an important role in driving plant dynamics and diversity.

Several studies have used insecticide and fungicide applications to assess the role of insects and pathogens in maintaining plant diversity and causing conspecific negative density-dependent plant survival as predicted by the Janzen-Connell hypothesis (e.g. Bell et al. 2006; Bagchi et al. 2014; Gripenberg et al. 2014; Fricke et al. 2014). However, to our knowledge, none of the insecticide studies have followed the fate of the seeds and seedlings in close enough detail to allow any conclusions to be drawn regarding which stage in the early life of plants was most likely to suffer from enemy mediated mortality, and how insecticide treatment would impact insect herbivores specific to these stages. Moreover, since most studies assessing the role of enemies on plant recruitment have applied insecticides and fungicides separately, little is known about the potential interactive effects of insect and pathogen attacks (e.g. Bagchi et al. 2014; Gripenberg et al. 2014).

The main objectives of this study were to investigate the impacts of insect herbivores and fungal pathogens on the early regeneration of a tree species of great importance in agroforestry in Central America and Mexico, *Guazuma ulmifolia* Lam. (Batis et al. 1999). *Guazuma ulmifolia* is one of the most common trees in agricultural areas in Central America, where it grows in fields, primary and secondary forests (Orwa et al. 2009). Elucidating the major causes of mortality of this species at an early stage can help in drafting recommendations to foster the regeneration of this species and forest reestablishment during the process of rehabilitation of degraded soils (Griscom et al. 2009).

Our protocol involved assessing both the damage on seeds caused by insect predators and the potential joint effects of insect herbivores and fungal pathogens on seed germina-

tion and the survival of young seedlings. We then evaluated (1) which stage (seed, seed-to-seedling transition, seedling) is particularly vulnerable to insect herbivores and pathogens; (2) whether the negative impact of insect herbivores at the seedling stage is higher than that of fungal pathogens; and (3) whether seed or seedling density affects the action of insect herbivores and fungal pathogens, as predicted by the Janzen-Connell hypothesis (Alvarez-Loayza and Terborgh 2011). Finally, with these data in hand, we briefly discuss their implication for the regeneration of *G. ulmifolia* in agroforestry landscapes of Central America.

Material and methods

Study sites

Insect seed predators were reared from *Guazuma ulmifolia* fruits collected on Barro Colorado Island (BCI) and at a nearby site, El Charco (ELC). As the use of insecticide is not allowed on BCI, our experiment assessing the role of insects and pathogens at the seed-to-seedling transition stage was conducted at ELC. Barro Colorado island is a biological reserve (9.15N, 79.85W, elevation 120–160 m) of 1,500 ha covered by lowland rainforest and created by the opening of the Panama Canal in 1914. A permanent ForestGEO vegetation plot (Anderson-Teixeira et al. 2014) of 50 ha is located in the centre of the island. The annual average rainfall is 2551 mm and annual average daily maximum air temperature is 26.3 °C. Details about the island and the rainforest plot are reported in Anderson-Teixeira et al. (2014). ELC (9°502.58'N, 79°39048.24'W, elevation 100 m) is ca 20 km from BCI and is part of the 19,545 ha Soberania National Park. There is a one ha ForestGEO plot at ELC and salient differences between the vegetation on BCI and that of ELC and other ForestGEO plots in the area are discussed in Pyke et al. (2001). ELC is a secondary rainforest while BCI includes both mature secondary forest and old-growth forest. Annual average rainfall is also lower (2050 mm) at ELC than at BCI (Pyke et al. 2001).

Study plant

Guazuma ulmifolia (Lam. 1789, Malvaceae, "Guácimo" in Panama) was selected for this study because of the relatively high availability of seeds at the study sites. It is also an important tree species in agroforestry, being used for firewood, medical treatment, the production of living fences and rehabilitation of degraded soils by fostering forest regeneration (Batis et al. 1999; Griscom et al. 2009). Other advantages of selecting this species in the context of our study included long-lived seeds (+18 months, Sautu et al. 2006) and rather quick germination (10–143 days after sowing, Roman et al. 2012; average 52.5 days: Sautu et al. 2006).

Of the seven species in the *Guazuma* genus, *G. ulmifolia* is the only one to occur in Panama (Robyns and Cautrecasas 1964). The tree is 4–25 m tall, with a broad and

irregular crown and grey bark. It grows at low or medium elevation, in lowland dry or wet forests, from Mexico to Paraguay, most commonly in areas where annual rainfall is 700–2500 mm (average 1,956 mm), and in a variety of soils (Francis 1991; CONA-FOR 2018). In Panama, it is commonly observed on the Pacific side, where it flowers and produces fruits from January to July. The species is partially deciduous during the dry season (Roman et al. 2012). *Guazuma ulmifolia* is a pioneer species and usually constitutes only a small percentage of basal area in secondary forests (Francis 1991). On BCI, the 50 ha plot of old growth forest includes 64 individuals of this species (Forest GEO 2018). At ELC *G. ulmifolia* is not present in the small one ha plot (and was also not recorded within or near our experimental blocks) but is relatively frequent nearby (i.e., within 500 m).

Individual *Guazuma* trees can produce up to 5,000–10,000 fruits per crop. The capsule of the fruit is elliptical or hemispherical, measuring between 18–25mm long, and 14–22mm wide. When mature, it is black (Suppl. material 1: Plate S1), contains a hydrophilic mucilage, and includes 60–68 small seeds averaging 2 mm length and 0.0042 g dry weight (Robyns and Cautrecasas 1964; Francis 1991; Roman et al. 2012). Fruits usually mature from September to April and may be observed for long periods on trees (Batis et al. 1999). Fruits are eaten by peccaries, tapirs, deer, agoutis and squirrels, as well as domestic livestock; bats are efficient seed dispersers (Janzen 1983; Roman et al. 2012). In Mexico and Costa Rica 12–42% of seeds have been reported to have been destroyed by several species of bruchine beetles (Johnson and Kingsolver 1971; Janzen 1975, 1983).

Insect rearing from seeds

For rearing insects we collected 320 fruits freshly fallen (without apparent decomposition) from *G. ulmifolia* on BCI. They were obtained between 2011–2013 from 22 trees (average 14.5 fruits collected per tree). To assess pre-dispersal attack (i.e., while seeds are still on trees) of *G. ulmifolia* fruits, in 2016 we collected 100 fruits directly from the crown of 5 trees near the 1ha plot in ELC (20 fruits collected per tree). In both cases fruits were stored in individual plastic pots, lined with tissue paper and covered with 1 mm mesh netting for ventilation and to avoid subsequent colonization/contamination of fruits. Rearing pots were checked twice weekly, and any emerging insects were collected, preserved, mounted and then identified with the assistance of taxonomists (see Acknowledgements) and/or with molecular techniques (Ratnasingham and Hebert 2013). Fruits were stored for 3 months and then dissected to check for the presence of developing larvae. We obtained DNA Cytochrome c oxidase subunit I (COI, 'DNA barcode') sequences from legs of representative insect specimens and we used Barcode Index Numbers (BINs) derived from insect sequences to delineate species (Ratnasingham and Hebert 2013). Molecular data were uploaded in the Barcode of Life project "BCISP" (http://www.barcodinglife.org/). Insect vouchers were deposited at the Fairchild Museum and Smithsonian Tropical Research Institute in Panama.

Monitoring of seeds and seedlings

Ten experimental blocks (B01 to B10) were set up near the permanent plot at ELC (coordinates in Suppl. material 1: Table S1; the distance between blocks varied from 16 to 69 m). Each block (5.5m × 2.5m) consisted of 8 quadrats of 1 m², in which 4 treatments were applied to two seed densities (10 and 25 seeds per m², see below). Control quadrats (coded C10 and C25) were sprayed with water, insecticide quadrats (I10 and I25) were sprayed with insecticide, fungicide quadrats (F10 and F25) were sprayed with fungicide, and combined treatment quadrats (I+F10 and I+F25) were sprayed with insecticide and fungicide. Quadrats (one replicate of each treatment combination per block) were located at random within each block (Suppl. material 1: Table S1). Litterfall traps on BCI (Wright et al. 2004) were used to estimate natural *G. ulmifolia* seed densities. In 2013, average seed density of *G. ulmifolia* at ELC was 1 seed m^{-2} y^{-1} (n=50 traps, L. Markesteijn and O. Lewis unpubl. data). On BCI, for the period 1987–2011, seed density for this species was 6.1 seeds m^{-2} y^{-1} (n=200 traps, Wright et al. 2004; S.J. Wright unpubl. data). The density of seeds buried in the soil was much lower, < 0.6 seeds m^{-2} (Dalling et al. 1997). Hence for our experiment we considered a high natural seed density of 10 seeds m^{-2} y^{-1} and a very high seed density of 25 seeds m^{-2} y^{-1}.

We used the insecticide ENGEO 247 SC (Syngenta SA, Basel, Switzerland) with active ingredients thiamethoxam (a neonicotinoid) 141 g L^{-1} and lambda-cyhalothrin (a pyrethroid) 106 g L^{-1}. According to the manufacturer, thiamethoxam has root-, leaf- and stem-systemic activity, while Lambda-cyhalothrin has a strong contact action. We used 0.0025ml m^{-2} in 50 ml sprayed on each quadrat every week, as recommended by the manufacturer and used in previous studies (e.g. Bagchi et al. 2014). ENGEO is a broad-spectrum insecticide, commonly used against herbivorous insects in crops. At the volume used here, ENGEO has very few ecotoxic and health risks. Similarly, we used the fungicide AMISTAR TOP 325 SC (Syngenta SA, Basel, Switzerland), with active ingredients difenoconazole 125 g L^{-1} and azoxystrobin 250 g L^{-1}. AMISTAR was sprayed at levels of 0.1ml m^{-2} in 1000 ml on each quadrat every week, as used by Bagchi et al. (2014) and at a slightly higher level than recommended by the manufacturer (0.05 ml m^{-2}). Difenoconazole is a broad-spectrum fungicide, while azoxystrobin is a systemic fungicide commonly used in agriculture.

In total, 1,400 fresh seeds of *G. ulmifolia*, collected from different trees near ELC, were sown into the experimental blocks in May 2016 at the onset of the rainy season. Prior to sowing, capsules were opened and seeds were checked for insect damage. Only apparently intact seeds were sown. To mimic near natural conditions, seeds were not treated to increase germination rates (Sautu et al. 2006). Blocks were first cleared of litter and seeds, and seeds of *G. ulmifolia* were then sown and the litter carefully replaced. Within each quadrat seeds were sown individually in 25 areas of 20 × 20 cm delineated by a sowing frame. In quadrats with a seed density of 10 seeds m^{-2} y^{-1}, seeds were positioned in 10 randomly selected 20 × 20 cm areas, whereas at a seed density of 25 seeds m^{-2} y^{-1}, each seed occupied one of the 25 areas. Each seed was coded and marked with a plastic coffee stirrer for the purpose of monitoring. After sowing, each quadrat was

sprayed weekly with a hand mister with 50 ml of water (control) or with 50 ml of the corresponding treatment for a total duration of 14 weeks (to August 2016). After this date surviving seedlings were measured and monitored at a lower frequency until May 2017, one year after the start of the experiment. Every week, the status of each seed or seedling was scored individually as Seed (no germination), Seedling (germination occurred, seedling growing, no insect damage), Damaged (seedling growing with damage) and Dead (seedling germinated but subsequently died). We initially planned to score seedlings in the Damaged category further using 10 different subcategories (including chewing, mining, galling, skeletonizing, etc.), but only three of these categories proved to be useful for *G. ulmifolia* seedlings: (a) leaf chewing (on side of leaves; possible agents Lepidoptera and Orthoptera); (b) shrivelled and/or necrotic areas (possible agent: fungi); and (c) unknown reason (i.e., damage could not be attributed with certainty). Seedlings of species other than *G. ulmifolia* were removed from quadrats throughout the monitoring period. At the end of the experiment, we measured the height of surviving seedlings.

Statistical analyses

We first ensured that there was no or little spatial pseudoreplication in our data by running simple Mantel tests (1,000 randomizations) between the dependent variables (see below) and the coordinates of the blocks. There was no obvious spatial autocorrelation for any of the response variables: germinated seeds: Mantel's t = 0.092, p = 0.303; dead seedlings: t = 0.117, p = 0.248; damaged seedlings: t = -0.079, p = 0.654. We used general linear models (GLM) to test the effect of treatment (Control, Fungicide, Insecticide and Insecticide + Fungicide), seedling density (10 or 25 seeds) and the interaction between these two fixed effects on the three dependent variables, at the end of the 14 monitoring weeks: number and percentage of germinated seeds, seedling mortality (number and percentage of dead seedlings) and number and percentage of seedlings damaged. All statistical analyses were conducted using R v 3.3.3 (R Development Core Team 2011) in the RStudio (Racine 2012) integrated development environment. The glm function was used with dependent variables expressed as percentages to compare the two seed densities. The significance of each fixed effect in the GLMs was assessed using the Anova function of the package 'car' in R (Fox and Weisberg 2017) and is provided in the Results section together with the likelihood-ratio chi-square (LRχ^2) and the corresponding degrees of freedom. We empirically modelled seedling survival over time with a rational model (y = (a + b * x) / (1 + c * x + d * x^2); where y is the number of seedlings growing and x is the time in weeks), which in almost all cases tested had the highest coefficient of determination (R^2) and the lowest Akaike information criterion corrected (AICC) of all models tested with CurveExpert Professional (Hyams 2011). We tested significant differences between fitted models using Kolmogorov-Smirnov two samples tests. We used available rainfall data from BCI (http://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado) to check for possible correlation with the mortality of seedlings at ELC. Means ± s.e. are reported in text and figures.

Results

Insects reared from fruits

The insects reared from the fruits of *G. ulmifolia* are summarized in Table 1, notes on their ecology are presented in Appendix S1, and some species are illustrated in Plate S1. They included 15 species, mostly Coleoptera. Six beetle species (four Bruchinae, *Amblycerus* spp. and two Anobiinae, *Lasioderma* spp.) can be considered as seed predators, are likely to be host-specific to *G. ulmifolia* and represented 69% of individuals reared. Further, one lepidopteran seed predator was also reared and considered to be generalist (Appendix S1). The percentage of Anobiinae to the total number of insects reared was higher at ELC (90%) than at BCI (38%). Faunal differences between ELC and BCI may partly be due to pre- and post-dispersal fruit attack as the percentage of fungal-feeders, scavengers or sapromycetophagous insects reared was higher at BCI (26.3%) than at ELC (5.4%). At ELC, out of the 100 fruits obtained from trees and reared (i.e., pre-dispersal stage), 92% of fruits were attacked by Anobiinae.

Seed germination

After 14 weeks of monitoring, 36.1% of the 1,400 sown seeds had germinated (Suppl. material 1: Table S2). Peak germination occurred during the onset of the rainy season, in the third week of monitoring (24.1%). The average percentage of germinated seeds per block ranged from 30.8% (quadrats I25) to 42.0% (quadrats F10) but varied little between treatments and seed densities (Fig. 1; Suppl. material 1: Table S2). This was confirmed by the GLM, which indicated no significant effect of combined insecticide and fungicide treatment on germination ($LR\chi^2 = 0.17$, df = 3, p = 0.98), seed density ($LR\chi^2 = 1.57$, df = 1, p = 0.20), or their interaction ($LR\chi^2 = 1.30$, df = 3, p = 0.72).

Survival, growth and mortality of seedlings

Overall, seedling mortality was very high, and in total 95.7% of germinated seeds were dead by Week 14 (Suppl. material 1: Table S3). Average seedling mortality (percentage of dead seedlings to total germinated seeds) per block varied little and ranged from 88.6% in quadrats F25 to 97.8% in quadrats I10 (Fig. 2). GLM models confirmed that (a) treatments had no effect on the survival of seedlings ($LR\chi^2 = 5.24$, df = 3, p = 0.15); (b) seed densities had no effect on seedling survival $LR\chi^2 = 0.0048$, df = 1, p = 0.94); and (c) the interaction between the two variables had no impact on seedling survival ($LR\chi^2 2 = 1.30$, df = 3, p = 0.72). Seedling survival over time could be fitted to rational models (Fig. 3; range of R^2 0.899 to 0.968). At densities of 10 seeds per m², seedling survival was similar in control and I10 quadrats. However, it was slightly better in F10 quadrats than in control quadrats and this difference was significant

Table 1. Summary of insects reared (total number of individuals per species) from fruits of *G. ulmifolia* at BCI (320 fruits) and ELC (100 fruits). Barcode Index Number (BIN) indicated when available and is linked to available insect pictures. Host specificity was inferred from a larger study on insect seed predators on BCI (Gripenberg et al. 2018).

| Taxa	BIN	BCI	ELC	Notes
Coleoptera				
Chrysomelidae – Bruchinae				
Amblycerus cistelinus (Gyllenhal, 1833)	BOLD:ACG0463	72	0	Seed predator, host specific on *G. ulmifolia*
Amblycerus sp. bru39SG	BOLD:ACJ3956	39	3	Seed predator, host specific on *G. ulmifolia*
Amblycerus sp. bru30SG	BOLD:ABW8381	15	0	Seed predator, host specific on *G. ulmifolia*
Mimosestes sp. 1YB	–	0	1	Seed predator
Ptinidae – Anobiinae				
Lasioderma sp. ano2SG	BOLD:ACF0770	242	291	Seed predator, host specific on *G. ulmifolia*
Lasioderma sp. ano4SG	–	1	0	Seed predator
Bostrichidae				
Lyctus sp.	–	0	2	Wood borer
Silvanidae				
Ahasverus advena (Waltl, 1832)	–	1	0	Fungal-feeder, cosmopolitan pest of stored products
Cathartus sp. 1SG	–	115	0	Probably fungal-feeder
Unidentified ELC sp. 1	–	0	1	Probably fungal-feeder
Unidentified ELC sp. 2	–	0	1	Probably fungal-feeder
Cucujidae				
Unidentified – cuj1SG	–	63	0	Ecology unknown
Nitidulidae				
Stelidota sp. 5SG	–	2	0	Sapromycetophagous?, generalist, reared from several hosts
Unidentified larva	BOLD:ACL7065	29	0	Sapromycetophagous?, may be larvae of *Stelidota* sp. 5SG
Stelidota sp. 6SG	–	0	1	Sapromycetophagous?, generalist, reared from several hosts
Curculionidae – Scolytinae				
Xyleborus sp. 1YB	–	0	1	Wood borer
Corylophidae				
Unidentified Corylophidae	–	0	11	Fungal-feeder
Lepidoptera				
Autostichidae				
Deoclona xanthoselene (Walsingham, 1911)	BOLD:ACF0463	51	0	Seed predator, generalist, reared from several hosts
Blastobasidae				
Blas lep37SG	BOLD:ABV2151	2	1	Scavenger, generalist, reared from several hosts
Blas lep31SG	BOLD:ABV2158	1	2	Scavenger, generalist, reared from several hosts
Hymenoptera				
Braconidae				
Unidentified Braconidae	–	0	1	Parasitoid
Pteromalidae				
Unidentified Pteromalidae	–	1	7	Parasitoid
TOTAL		**634**	**323**	
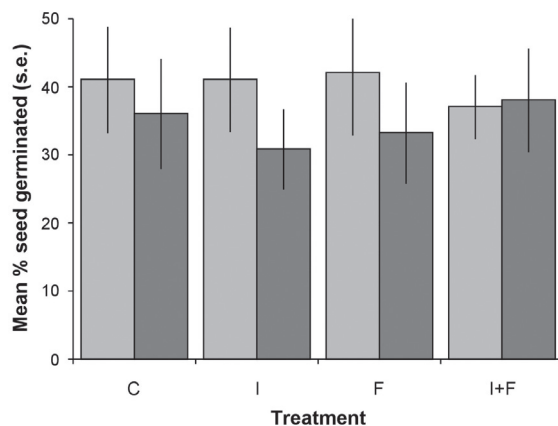
Figure 1. Average percentage of germinated seeds per block, detailed by treatment (C = control, I = insecticide, F = fungicide, I+F = insecticide and fungicide) and seed densities (light bars: 10 seeds m^{-2} y^{-1}; dark bars: 25 seeds m^{-2} y^{-1}).
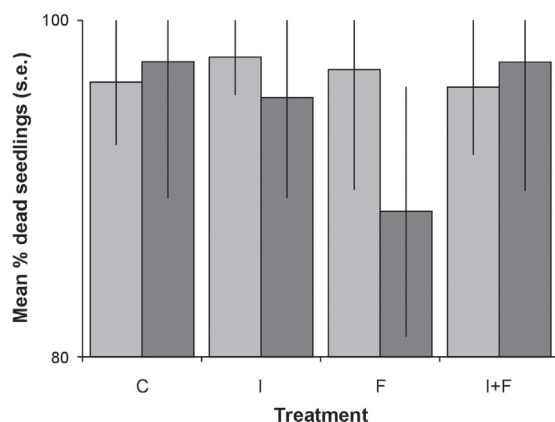

Figure 2. Average percentage of dead seedlings per block, detailed by treatment (C, I, F, I+F, coded as in Fig. 1) and seed densities (light bars: 10 seeds m^{-2} y^{-1}; dark bars: 25 seeds m^{-2} y^{-1}).

(Kolmogorov-Smirnov two samples test between the two fitted models, max. diff. = 0.267, p = 0.002). Patterns of survival of seedlings were similar when sown at densities of 10 seeds per m^2 or 25 seeds per m^2. At densities of 25 seeds per m^2, seedling survival was higher in F25 quadrats than in control quadrats (max. diff. = 0.327, p < 0.0001), and also slightly higher in I+F25 quadrats than in control quadrats (max. diff. = 0.228, p = 0.011). However, these differences were small (Fig. 3).

The highest seedling mortality was in weeks 4 and 5 (weeks of the 27 May and 3 June 2016), with a total of 77 and 86 dead seedlings, respectively. During week 4, only one week after the highest rate of seed germination (Fig. 3), 25.7% of seedlings growing the preceding week died. Weekly seedling mortality was not correlated with the
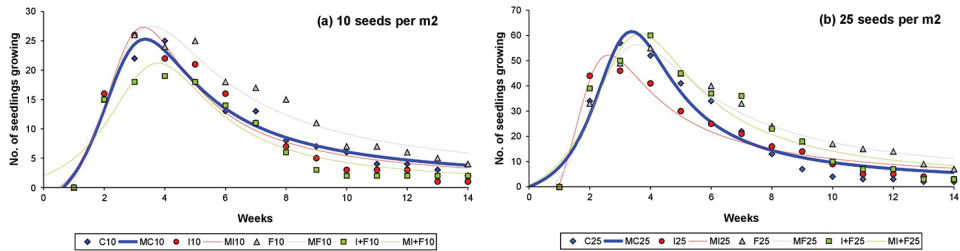
Figure 3. Number of seedlings growing plotted against time for each treatment (coded as in Fig. 1 and plotted with different colors) and seed densities of **a** 10 seeds per m² and **b** 25 seeds per m². Observations indicated by symbols, fitted rational models indicated by continuous lines (control identified by thick blue line).

amount of rainfall every monitoring week (r = -0.08, p > 0.80; excluding weeks 1 and 2 during which few seeds germinated and no seedlings died). However, the cumulative mortality of seedlings during weeks 3 to 14 was strongly and positively correlated with the cumulative amount of rainfall during the same period (r = 0.93, p < 0.0001).

After 14 weeks of monitoring, only 24 seedlings were alive, including 9 damaged seedlings, spread only over 4 blocks. The rational models estimated that after one year of monitoring, a total of 9 seedlings for the whole experiment would still be alive. This was not the case: the last two seedlings died on 5 May 2017, one year after the beginning of the experiment, in block 07, quadrat I+F25. The growth and biomass of surviving seedlings in week 14 were also rather slow and low. They measured on average 30.0 ± 1.91 mm and the two last seedlings to die were 125 and 140 mm tall. Since the sample size of surviving seedlings in week 14 was low, we performed a simple ANOVA that indicated that neither treatment ($F_{3,1}$= 0.896, p = 0.48) nor seed density ($F_{3,1}$= 0.713, p = 0.42) had any effect on seedling height.

Damage to seedlings

Overall, 100 out of 506 seedlings that germinated were damaged (19.8%, Suppl. material 1: Table S4). In 80% of cases, damage was identified as originating from leaf-chewing insects, 19% of cases involved fungal necrosis, whereas the final 1% could not be attributed with certainty. The mean percentage of damaged seedlings relative to total germinated seeds per block varied from 15.5% (F10) to 25.2% (C10), with no clear positive effect of insecticide (Fig. 4). GLM models indicated that neither the combined insecticide and fungicide treatment (LRχ^2 = 0.60, df = 3, p = 0.89), nor seed density treatments (density (LRχ^2 = 0.27, df = 1, p = 0.60), nor their interaction (LRχ^2 = 0.26, df = 3, p = 0.98) had a significant effect on the number of damaged seedlings. The relatively low percentage of seedlings damaged, as compared to the mortality of apparently undamaged seedlings (80.2%), suggests that insects were not responsible for most seedling mortality. This was confirmed by the rarity with which insects were observed damaging seedlings during day-time fieldwork.
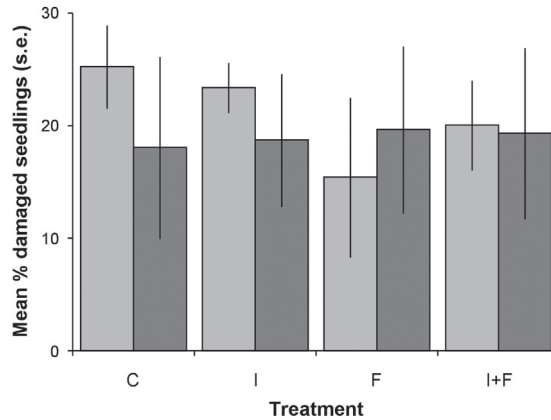
Figure 4. Average percentage of damaged seedlings per block, detailed by treatment (C, I, F, I+F, coded as in Fig. 1) and seed densities (light bars: 10 seeds m^{-2} y^{-1}; dark bars: 25 seeds m^{-2} y^{-1}).

Discussion

Which stage is particularly sensitive to insect herbivores?

Regarding this question, we observed that: (a) pre-dispersal attack of the fruits of *Guazuma ulmifolia* is very high (up to 92% of fruits attacked) and the result of the action of several species of insect seed predators, mainly anobiine and bruchine beetles (*Lasioderma* spp. and *Amblycerus* spp.). (b) In Panama, and contrary to what was observed in Costa Rica (Janzen 1975), anobiine beetles were responsible for most of the fruit damage, not bruchine beetles. (c) Post-dispersal attack of isolated *G. ulmifolia* seeds appears to be rare, as rates of seed germination (overall 36%) were not affected significantly by either insecticide or fungicide treatments, nor by seed density. (d) Once seeds germinated, seedling mortality was high (> 95% after 14 weeks of monitoring) but was not reduced by our insecticide or fungicide treatments and was not affected by seed density.

Because of very high pre-dispersal attack of *G. ulmifolia* fruits at ELC, the number of viable seeds that can germinate on the ground is probably considerably reduced. Janzen (1975) indicates that in Costa Rica in almost all *G. ulmifolia* fruits attacked by *Amblycerus cistelinus*, all seeds in the fruit are destroyed by the time the larva matures. The same author reports that anobiine beetles drill through large number of seeds but that they rarely kill > 50% of the seeds in a fruit and infest usually < 5% of fruits in the field. Although we have no precise rate of seed attack per se, it presumably remains high because of the high infestation rate of fruits and should be a strong limiting factor in the early regeneration of *G. ulmifolia* at ELC. The distance to other reproductive conspecific trees, as well as the dispersal distance of insect seed predators, could also explain different rates of fruit attack per tree (Janzen 1975), but this was not quantified in this study. Fruits stay on trees for a long time; they are dormant and immature

for 5–6 months and then mature over 3 months (Janzen 1982). *Amblycerus* spp. attack fruits when maturing (Janzen 1975), but long periods of fruit exposure on trees may be favorable to other seed predators, such as anobiine beetles.

In contrast, we believe that post-dispersal attack of *G. ulmifolia* seeds by insects is infrequent. *Amblycerus* spp. do not oviposit on fallen fruits even if there are many on the ground (Janzen 1975). Our insecticide treatment did not affect the rate of germination of isolated seeds, which anyway are small and hence unlikely to be attacked by insects (Moles et al. 2003). Although *G. ulmifolia* seeds lack polyphenols as defensive compounds, they invest in protective tissue, as almost 70% of the seed dry weight is made up by a hard seed coat (Gripenberg et al. 2018; S. Gripenberg, pers. obs.). This could further impede the attack on isolated seeds. Furthermore, the lack of improved seed germination or seedling survival in our insecticide and fungicide treatments (see below) suggests that the pre-dispersal seed stage is by far the stage most sensitive to insect enemies.

Is the negative impact of insect herbivores at the seedling stage higher than that of fungal pathogens? Agents of seedling mortality

In relation to this question we further observed that: (a) seedling survival over time was weakly and positively influenced by the fungicide treatment. (b) There was a strong positive correlation between weekly cumulative seedling mortality and cumulative rainfall. (c) About 20% of seeds that germinated were damaged, mostly by leaf-chewing insects, but neither the treatments nor seed density affected the number of damaged seedlings. (d) Insect herbivores were not observed feeding on seedlings during day-time. (e) Seedling growth was slow (3cm tall after 14 weeks), and all 506 seedlings that germinated out of 1,400 seeds sown were dead after one year.

Leaves of *G. ulmifolia* on mature trees are readily attacked by a variety of insect herbivores (Janzen 1983), but reports of damage on conspecific seedlings are, to the best of our knowledge, not available. Insects feeding on *G. ulmifolia* seedlings may be active during night-time, as suggested by the low but nevertheless standing leaf damage suffered by seedlings (16% of germinated seeds). It is also unlikely that seedling mortality could be explained by the near presence of conspecific mature trees and contagion of insect herbivores, as *G. ulmifolia* is not very common at ELC. These arguments, along with the lack of insecticide treatments on the survival of seedlings or their damage, suggest that insect herbivores (leaf-chewing and sap-sucking insects) infrequently attacked *G. ulmifolia* seedlings at ELC, and are not primarily responsible for seedling mortality. This could be explained by the low foliar biomass represented by these seedlings (Basset 1999).

Apart from a weak positive effect of fungicide treatment on seedling demography (survival in time; as reported in Bagchi et al. 2014), our data do not provide evidence for fungal pathogens being important in the early regeneration of *G. ulmifolia*. When seedlings were damaged, and the source of damage could be unequivocally scored,

more seedlings were apparently damaged by insects rather than by fungi. However, it may be very difficult to score visually seedlings damaged by fungi. Furthermore, our fungicide treatment may have been more effective against endophytic pathogens than soil pathogens, which may attack both seeds and seedlings (Mangan et al. 2010). The lack of fungicide effects may also be explained differently. Strobel et al. (2007) reported on a strain of *Muscodor albus* isolated in leaves of *G. ulmifolia* in Ecuador and able to colonize conspecific seedlings. This endophytic fungus produces a series of volatile organic compounds with antibiotic activity that collectively act to kill other fungi or bacteria, while there are no external symptoms on its host. It may be argued that this fungus lives in its host in a symbiotic condition, providing protection from pathogens while surviving and growing on plant nutrients (Strobel et al. 2007). If *G. ulmifolia* produces its own fungicides, then the lack of strong effect of our fungicide treatment is not surprising.

July 2016 should have been a period of active growth for *G. ulmifolia* seedlings that germinated in May 2016. July 2016 was the second rainiest July (monthly sum 486.8mm) on BCI since records began in 1925, only surpassed by July 1956 (496.6mm; http://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado). In these conditions, high rainfall may have caused soil anoxia and some rot in seeds and seedlings, as suggested by the strong correlation between cumulative rainfall and seedling mortality during the experiment. Further, *G. ulmifolia* seedlings have a relatively low tolerance to flooding (Lopez and Kursar 2003), and heavy rain may also damage stems and foliage or uproot the seedlings. Thus, we strongly suspect that the main agent of seedling mortality during the experiment was unfavorable rainfall conditions, but we stress that the patterns recorded may not apply under all conditions.

Does seed or seedling density affect the action of enemies? Relations with the Janzen-Connell hypothesis

For the densities considered in this study, post-dispersal seed and seedling density did not greatly affect the negative action of insect herbivores and fungal pathogens. The lack of difference in seedling survival between control quadrats sown at two different seed densities also suggests that intra-specific competition of seedlings is not responsible for their high mortality (Alvarez-Loayza and Terborgh 2011), at least for the densities considered in this study, which were high as compared to natural seed densities for this species in Panama.

Since post-dispersal attack of *G. ulmifolia* seeds and seedlings by insects at ELC was infrequent, this suggests that Janzen-Connell effects due to insect herbivores specifically, if they exist, may be rather weak for this tree species. Comita et al. (2010) examined the strength of negative density-dependence for 180 plant species on nearby BCI, investigating seedling survival as function of conspecific seedling abundance (Suppl. material 1: Table S2 in Comita et al. 2010), they found that the strength of conspecific neighbor effects were rather weak for *G. ulmifolia*, which ranked 158th

out of 180 species (i.e. in the lower quartile of species). Nonetheless their data indicate negative density-dependence for *G. ulmifolia*, raising the question of which biotic agent may be responsible.

Since *Amblycerus* spp. only oviposit in fruits on trees (Janzen 1975), they are probably not involved directly in this negative density-dependence. Perhaps a more plausible explanation is that rapid ingestion of *G. ulmifolia* fruits by dispersal agents (mammals, birds and bats; Janzen 1982) results in small clusters of seeds, germinating close together corresponding to a single defecation (Howe 1989; Lawson et al. 2012). Seeds and seedlings would be unlikely to be attacked by insects, as suggested by our experiment, and these clusters are potentially very isolated from other conspecifics (Lawson et al. 2012).

Possible biases in our study

First, as indicated by further monitoring of blocks after 14 weeks, seeds were unlikely to germinate after the end of our experiment. This suggests that the length of the study and the germination rate of seeds were appropriate for our experiment (and see Gripenberg et al. 2014). Yet, the overall growth of seedlings was slow: after nearly 4 months of monitoring, most seedlings were dead and survivors were < 5cm tall, whereas in greenhouse conditions after the same time period, seedlings are usually 30–40 cm tall (Francis 1991). Seedling biomass, not measured in the present study, was presumably low with, on average, only 3–5 leaves amounting to 4 cm^2 for each survivor at the end of the experiment. Further, seedlings survived only a short time at ELC: 27.5% of germinated seedlings survived only one week. In these conditions, selecting a different tree species for our experiment, with rapid growth and high foliar biomass, would have perhaps helped to quantify better seedling mortality due to insect herbivores.

Second, the overall germination rate of *G. ulmifolia* seeds (36%) was higher at ELC than that reported in the literature for Panama (natural conditions, 20%: Sautu et al. 2006). Many seeds germinated quickly, within three weeks of being sown. This suggests that light limitation at ELC was not a major factor compromising seedling performance of *G. ulmifolia* at the early stages of the life cycle of this species, which was the focus of our study. Indeed, this pioneer species can grow in a variety of habitats (Francis 1991), but we acknowledge that (1) our experimental conditions might have been different from open habitats where *G. ulmifolia* also grows and (2) that the longer-term survival of the seedlings and saplings of this species might be compromised by limited light. Whether light-demanding pioneers are ultimately able to grow to maturity in a given location will depend on changes to the light environment *subsequent* to establishment. In a longer-term perspective, light gaps will form in the forest subsequent to seedling establishment, providing initially shaded seedlings with the conditions necessary to grow towards maturity. Thus, it is relevant to look at the early stages of seedling growth under relatively shaded conditions because the outcome of this phase in plant demography sets the template for future establishment.

Third, an unknown proportion of seeds was also probably lost in our experiment before germination. We observed damage due to vertebrates crossing the blocks (i.e., excavated soil, seed labels chewed), most likely caused by agoutis, *Dasyprocta punctata*, and coatis, *Nasua narica*. We also suspect that ants, particularly *Atta* spp., removed some of the seeds used in the experiment. In Colombia, several ant species, such as *Atta cephalotes*, are known to remove preferentially in open pastures small tree seeds including *G. ulmifolia* (Escobar-Ramírez et al. 2012). On BCI, a high proportion of *G. ulmifolia* seeds are removed secondarily, presumably by ants (Ruzi et al. 2017). However, our insecticide treatment at ELC should have impacted negatively such seed removal by ants. Heavy rainfall may have also washed some of the small seeds out of the experimental blocks. The very small size of the seeds made it impossible to search for individual seeds at the end of the experiment and assess their fate. Selecting tree species with large seeds would thus be useful for future experiments. We believe that pre-germination loss to vertebrates is probably infrequent because of the low biomass represented by isolated seeds, but we cannot quantify loss of seeds due to removal by ants or by rainfall.

Our factorial design insured that all treatment groups were exposed to the same experimental conditions. All experimental blocks were thus likely to be affected in the same way by additional environmental factors (such as light conditions, seed removal by vertebrates and rainfall) which were not controlled in our study.

Conclusion

Our study generated new information on the role of natural enemies in the survival of *Guazuma ulmifolia* at the early stages of the life cycle. We conclude that the pre-dispersal seed stage is by far the stage most vulnerable to insect enemies. Also that the main agent of seedling mortality during the experiment was probably inclement rainfall, and that Janzen-Connell effects that may be specifically due to insect herbivores are probably rather weak for this tree species. The regeneration of *G. ulmifolia* in the forest of ELC appears to be difficult to account for but not to be the outcome of the action of insect herbivores after seeds are dispersed. This illustrates that each tree species may respond differently to pathogens and herbivores (Gripenberg et al. 2014), and that further work should aim at tracking the possible existence of suites of species that share a common response, perhaps partly dictated by conserved morphological and chemical traits (Paine et al. 2012).

What are the implications of our findings for the regeneration of this important tree species in agroforestry? Without addressing what may be suitable conditions for seedling growth, the regeneration of this species may further depend on effective primary dispersal of seeds by vertebrates before most of the seed crop is lost to insects. In this situation, local conservation of dispersal agents may be crucial to enhance escape of seed predation by insects. For example, artificial roosters for frugivorous bats, which disperse seeds of *G. ulmifolia* (Roman et al. 2012), may greatly help the regeneration of this species and the reestablishment of vegetation in disturbed areas (Silveira et al. 2011).

Acknowledgements

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Supplementary material 1

Supplementary tables S1-S4, Appendix S1, Plate S1

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