MACROECOLOGICAL PATTERNS OF PLANT SPECIES AND ANTHROPOGENIC ACTIVITIES

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

(Signature) …………………………………………………………………………

ABSTRACT

The study of macroecology not only identifies patterns in the distribution and abundance of species at large spatial and temporal scales, it also gives insight into the processes underlying those patterns. The contribution of this work is not limited to helping develop the field of ecology per se, but also provides important insights into the understanding of large scale processes like climate change, the spread of introduced species, pest control and how increasing pressure from anthropogenic activities threatens biodiversity and ecosystem services. During the first decade following its formal inception, most of the progress in macroecology was made through studies of animal species, and research into plant species continues to lag far behind. This thesis contributes to the study of the macroecology of plant species by examining some selected macroecological patterns that have been studied only for animal species and by including an important issue that might have significant effects on diverse macroecological patterns, namely anthropogenic activities.

The second and third chapters of the thesis address the generalised individuals-area relationship (GIAR) and the patch individuals-area relationship (PIAR), two macroecological relationships not previously explored for plant species. I show for the first time the existence of negative GIARs at the intraspecific and interspecific levels in plant species, similar to those documented for animal species. Unlike animal species, I did not find a broadly consistent intraspecific PIAR in plant species; more than half of the tested species showed negative PIARs. The resource concentration hypothesis may help explain those positive PIARs that were observed.

The fourth chapter considers the effect of past human activities on current patterns of plant species richness at a landscape scale. Using a detailed database on the historical anthropogenic activities for Cornwall, U.K., I examine the relationship between species richness and the area covered by each historical land-use at two different spatial resolutions (10km x 10km and 2km x 2km). I find that at the 10km x10km scale human activities carried out since the 17th and 19th centuries explain an important proportion of the variation in current plant species richness. In contrast, a model at 2km x 2km scale with upland woods and the total land area of a grid cell explain only 5% of the variation.

The fifth and sixth chapters focus on how artificial light at night (ALAN), which has increasingly come to attention as a significant anthropogenic pressure on species, is interacting with the distributions of plant species. In the fourth chapter, I consider the plant family Cactaceae to determine the proportion of the global distribution ranges of species that is being influenced by ALAN, and how this changes with the size of these distribution ranges and over a 21-year period (1992 to 2012). I found that >80% of cacti species are experiencing ALAN somewhere in their distribution range, and that there is a significant upward trend in ALAN in the ranges of the vast majority of species. For the sixth chapter, I consider similar issues for the threatened plant species of Britain, exploiting new remote sensing imagery of nighttime lighting at a very fine spatial resolution (c.340x340m^2). Only 8% of Britain is free of artificial light at night and in consequence a high number of threatened plant species have a high proportion of their range under some influence of ALAN.

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INTRODUCTION

Macroecology is the study of the distribution and abundance of organisms on large spatial and temporal scales (Brown & Maurer 1989; Blackburn & Gaston 1998; Maurer 1999; Brown 1999; Gaston & Blackburn 2000) with the aim of understanding patterns and determinants of the broad-scale distribution of life across the planet (Blackburn & Gaston 2003). As Gaston and Blackburn (1998) and later Brown (1999) pointed out, this research program arises from the necessity of studying ecological and biological systems from a 'macro' point of view, by studying their emergent properties, which arise from interactions (not always additive) from the lower level structural units (e.g. individual organisms, local population and communities; Novikoff 1945, MacArthur 1972, Brown 1995, Blackburn & Gaston 2003). Macroecology emerges from the need to place the "microscopic" ecological findings (e.g. experimental ecological and molecular evolutionary studies) in a broader perspective, as most of the experimental ecological studies cannot simply be extrapolated to larger scales or even be generalised to different systems. In addition, there is a need for studies on the effects of anthropogenic activities at regional and global scales, for which experimental ecological studies cannot easily contribute given the difficulty to generalise across systems and to extrapolate the results to broader scales (Brown 1999, Gaston 2003).

A decade after the definition of Macroecology in 1989, an important amount of work had already been done in understanding some of the more traditional macroecological patterns (e.g. patterns occurring in the structure of the geographic ranges of species, species-range size distributions, abundance-

range size relationships, species-abundance distributions, individuals-area relationships, regional and global scale species richness relationships, species-body size relationships, abundance-body size relationships). A number of patterns had been studied for a broad range of groups of animal species, including relationships between species richness and a diverse array of environmental and positional variables (latitude, longitude, altitude and depth), species-range size distributions, geographical range abundance structures, abundance-range size relationships, species-abundance distributions, species-body size distributions, and abundance-body size relationships (e.g. Taylor & Gotelli 1994, Gaston 1994, Enquist et al. 1995, Brown et al. 1996, Willing & Gannon 1997, Bonfim et al. 1998, Diniz-Filho & Balestra 1998, Blackburn & Gaston 1998, Gaston 1998, Gaston et al. 1998, Kaufman & Willig 1998, Brown 1999, Lees et al. 1999, Lyons & Willig 1999, Gaston & Blackburn 1999, 2000, Murray et al. 1999, Pyron 1999, Ruggiero 1999, Bakker & Kelt 2000, Channell & Lomolino 2000, Diniz-Filho et al.2000, Gomez & Espadaler 2000, Maurer 2000, Murray & Dickman 2000, Rahnek & Graves 2000, Vaughn & Taylor 2000). The progress in macroecological knowledge also led to calls for improving methodological aspects of the discipline (e.g. Gaston and Blackburn 1997, 1999). Since its inception in 1989, the number of macroecological publications (considered as such after the discipline was conceived) has steadily increased (Figure 1). However, most of the insights into macroecology between 1989 and 2000 (when the second book about Macroecology was published; Gaston & Blackburn, 2000) were developed from the study of animal species. Indeed, most of the macroecological studies during the years of the consolidation of the discipline only considered animal species. During this period of time, only 3 out of 79 macroecological studies considered plants as a direct subject of study

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(Lupia et al. 1999, Murray et al. 1999; Murray & Westoby 2000), with 13 more which considered a mixture of plant and animal species.

Plants in macroecology

The macroecological literature of plant species continues to be depauperate when compared to other taxa. I conducted a search on ISI Web of Science to quantify the number of publications on the macroecology of plants and animals from 1989 until September, 2015. I also searched in three selected journals: Global Ecology and Biogeography, Journal of Biogeography, and Diversity and Distributions, to add any documents missed from the ISI Web of Science. However, I did not find additional articles to the original search, and therefore this did not add further information.

The results show that of the 1,224 studies published only 268 considered vascular plants, in contrast to 874 studies made on animal species (Figure 2, and Appendix 1 for string search).

A close review of the 268 papers considering vascular plants reveals that only 142 focus on the macroecology of plants as a central theme (Table 1). 30 studies consider plants as an indirect focus of study, focussing mainly on analysing diverse plant interactions, in particular animal-plant interactions. 9 articles consider a mix of different taxa (Table 1). Finally, 87 articles were highlighted because the word 'plant' was contained in some way (e.g. as a contrasting example of the patterns analysed) but were not actually interested in plants. In summary, only 11.6% of the macroecological studies found in this search focus on plant species.

The macroecology of plant species has generally focused on the spatial distribution of species richness (Lopez-Mata et al. 2012, Dubuis et al. 2011, Jones et al. 2013), including invasiveness (Lloret et al. 2004, Hamilton et al. 2005, Akasaka et al. 2012, Bartomeus et al. 2012, Chapman et al. 2014, Hui et al. 2014). The analysis of some patterns by analysing phylogenies has been a focus of attention, e.g. occupancy and range sizes (Prinzing et al. 2004), species diversity (Knapp et al. 2008, Yan et al. 2013), as well as the study of niches (Köckemann et al. 2009, Romdal et al 2013, Thuiller et al. 2005, Banta et al. 2012). The effect of climate change on diverse macroecological patterns of plant species has also been assessed (Pither 2003, Jansson 2003, Elser et al. 2010; Svenning & Sandel 2013). Likewise, some of the most traditional topics in the study of macroecology of animal species have been considered for plants, e.g. regarding rarity (Lesica et al. 2006), on range sizes (Channell & Lomolino 2000, Brändle et al. 2003, Pither 2003, Svenning and Skov 2004, Kreft 2006, Schurr et al. 2007), on latitudinal patterns (Weiser et al. 2007, Bannister et al. 2012), geographic ranges (Gaston 2003; Svenning & Skov 2004; Beck et al. 2006, Procheş et al. 2012; Guarino et al. 2012), and abundance-body mass relationships (McGill et al. 2007, McGill 2008, Andrew & Hughes 2008). There is also a particular focus on studies of allometry and biomass (e.g. Enquist et al. 1998, Guoet al. 1998, West et al.1999; Niklas & Enquist 2001, Enquist & Niklas 2002; Kerkhoff et al. 2005; Kerkhoff & Enquist 2006), and on studies related to macrophysiology (Cony et al. 2006; Chown & Gaston 2008; Chown et al. 2010; Laanisto & Niinemets 2015); see Figure 3.

Kinds of spatial macroecological patterns

Developments in macroecology and biogeography led Gaston et al. (2008) to distinguish three general sets of spatial patterns: intraspecific, interspecific and assemblage. Intraspecific patterns are described in the traits exhibited within individual species, reflecting their covariation with locational or environmental variables. Interspecific patterns reflect differences in the traits shown between different species, and occurring in different locations. Finally, spatial variation at assemblage level refers to patterns in the structure of given assemblages in different places. Intraspecific spatial patterns in plant species have been described for life history traits (Kerkhoff & Ballantyne 2003, Van Der Veken et al. 2007, Hamilton et al. 2005), invasiveness (Swenson & Enquist 2007, Chapman et al. 2014), population dynamics (Kluth & Bruelheide 2005) and genetic variation (Knight & Ackerly 2002, Banta et al. 2012, Theodoridis et al. 2013). Interspecific spatial patterns for plants have been identified in geographical range sizes (Lloret et al. 2004, Svenning & Skov 2004, Kreft et al. 2006, Köckemann et al. 2009, Laanisto et al. 2015b). Finally, the study of macroecological patterns in plant assemblages has focused on species richness (Whittaker et al. 2001, Bhattarai & Vetaas 2003, Hawkins et al. 2003, Oommen & Shanker 2005, Pautasso & McKinney 2007, Svenning et al. 2008, Procheş et al. 2012, Wilson et al. 2012, Michalet et al. 2015, Triantis et al. 2015), and on allometry and metabolic theory (Enquist & Niklas 2001, Belgrano et al. 2002, Kerkhoff & Enquist 2006, Newman et al. 2014). It is important to mention that not all studies of the macroecology of plant species can be clearly categorised in terms of intraspecific, interspecific or assemblage approaches. The study of macroecological patterns on plant species started a decade later than the studies on animal species, which gave researchers the opportunity to

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address macroecological questions with new statistical techniques, allowing them simultaneously to address a mix of spatial patterns. Some examples include a mix between an intraspecific (e.g. germination timing) and interspecific patterns (e.g. local abundances and distribution range sizes, Brändle et al. 2003), or between interspecific (e.g. distribution of hybrid types) and assemblage patterns (e.g. species richness, e.g. Guo 2014). It is important to highlight that the pioneer research that laid the foundations of macroecology (before the term was coined in 1989) is not considered in this search. For a compilation of publications that contribute to the themes and developed the conceptual groundwork of macroecology see Smith et al. (2014).

Macroecological patterns and people

These intraspecific, interspecific and assemblage patterns have traditionally been derived from the analysis of variation in the traits or other characteristics of species with environmental or positional gradients, lacking in general the inclusion of one very important variable: human activities (Gaston 2003, 2004, 2005, 2006). Humans alter not only the areas surrounding them but are also transforming the planet by modifying global patterns of climate (Manabe et al. 1980, 1981, Machta 1983, Peters 1988, Suárez et al. 2002), nitrogen deposition (Elliot 1986, Hargreaves et al. 1998, Matson et al. 2002), land use (Matthews 1983, Foley et al. 2005, Meyer & Turner 1992, Dale 1997, Fearnside 2000, Pielke et al. 2002), and soil composition (Van Breemen et al. 1982 , Ulrich 1983, Post & Kwon 2000, Bai et al. 2008). Therefore it seems likely that these anthropogenic processes will interact with environmental and positional gradients to alter natural macroecological patterns. Two groups of processes

have been proposed to explain macroecological patterns: capacity rules and allocation rules (Brown 1981). Capacity rules refer to the extrinsic processes that determine the capacity of the environment to support a species assemblage. Allocation rules refer to the intrinsic processes that determine the structure or composition of the assemblage. Influences of human activities on capacity rules include dramatic changes to landscape configurations at global scales through land conversion (e.g. mining, deforestation). Influences of anthropogenic activities on allocation rules have been explained by dividing these into entry rules, i.e. processes determining which species joins a particular system (e.g. speciation, immigration), exit rules, i.e. processes determining which species leaves the system (e.g. extinction, emigration) and transformations or changes caused by processes that act upon species while they are members of a particular set (referring to processes of change, e.g. in behaviour or evolutionary modifications, Kunin 1997, Gaston 2006). By transforming land to agriculture for instance, human activities have a direct impact on the number of individuals of the species contained in an assemblage (decreasing or increasing them), and alter the rate of emigration and immigration between the patches left as suitable habitat for the species. The omnipresence of humans in all the ecosystems of the planet can modify behaviour of some species and apply additional inputs to the evolutionary process; for instance when parasite-host interactions are modified due to climate change or invasiveness.

A rare exception in the inclusion of human activities in the study of macroecological patterns is perhaps the well-recognised positive correlation between species richness and human population density (Gaston 2005, Luck 2007). At broad geographical scales, an increase of species richness with

human population density has frequently been observed. This pattern has been tested for insects (Pautasso & Fontaneto 2008, Barbosa et al. 2010), fish (McKinney 2002, 2008), birds (Gaston & Evans 2004, Chown et al. 2003, Koh et al 2006, Evans et al. 2007, Hugo & Rensburg 2008), mammals (Vázquez & Gaston 2004), vertebrates in general (Moreno-Rueda & Pizarro 2007), and for plants (McKinney 2002, 2008, Pautasso & McKinney 2007, McKinney 2008). It has inevitably provoked much speculation as to the mechanism.

However, the number of studies considering human activities as a variable that might explain a proportion of the variation in macroecological models is small. Studies on plant species are no exception.

This thesis

In this thesis I seek to help to redress the imbalances in macroecological studies highlighted above. I examine some selected macroecological patterns in plants that have previously been solely or almost exclusively studied for animals, and I focus repeatedly on how human activities have shaped the state of macroecological variables and patterns in plants.

The thesis consists of five analytical chapters and a general discussion. For the second and third chapters, I focus on intraspecific and interspecific levels of analysis, assessing two very well described relationships in the macroecology of animal species that have never been analysed before for plants: the generalised individuals-area relationship (GIAR) and the patch individuals-area relationship (PIAR). The GIAR, documented in the second chapter (the first analytical chapter), describes the relationship between the

abundance of individuals of plant species and the size of the plot area from which those abundances were estimated (where those plots may often bear no relation to real habitat patches). In animal studies, negative GIARs are commonly reported, and have considerable implications for ecology and conservation. In the third chapter, I analyse PIARs, which describe the relationship between the abundance of a species and patch area from which it has been estimated, where the patch itself is a natural unit or has been artificially created, generally as a consequence of landscape fragmentation. The form of these relationships in studies on animal species varies, although a positive individuals-area relationship is commonly obtained. I examine PIARs for plant species in terms of the predictions of the equilibrium theory of island biogeography, the resource concentration hypothesis and the density compensation hypothesis, which have previously been examined in this context for animal species.

Considering the evidence that anthropogenic activities have deeply modified the landscape, in the fourth chapter I take an assemblage level approach and analyse the role of historical land use in shaping present-day plant species richness. At a landscape level the spatial distribution of habitats is key in the study of the effects of the legacy of human activities on current patterns of biodiversity. Nevertheless, this kind of approach remains poorly explored, mainly due to the lack of detailed data on past human activities and their impact on the land. Here I exploit the availability of a detailed characterisation of the history of the landscape of Cornwall, U.K.

The fifth and sixth chapters focus on determining how artificial light at night (ALAN), a relatively recent recognised worldwide pollutant, is interacting

with spatial patterns in the distributions of plant species, combining intraspecific, interspecific and assemblage level analyses. In the fifth chapter, I consider the Cactaceae family to determine the proportions of the global geographic ranges of species that are being impacted by ALAN, and how this interaction changes with the size of the species geographic range. At the assemblage level, I then examine the interaction between ALAN and spatial variation in species richness and what the trend of ALAN is within the distribution of the family through time (21 years of ALAN data available).

In the sixth and final analytical chapter, I analyse, at the interspecific level, the fine scale relationship between the distribution of threatened plants in Britain and ALAN, exploiting some of the new satellite imagery that has become available during my studies. At the assemblage scale, similar to the fourth chapter, I determine the interaction between ALAN and species richness. Finally, given the evidence of the high proportion of threatened plant species occurring within the boundaries of protected areas in Britain, I determine the extent of nighttime lighting in these areas.

In the final chapter, the discussion, I highlight some methodological issues regarding the studies of the macroecology of plant species, and I suggest what is necessary to do to improve its study.

Finally, during the course of my studies, I collaborated in a study assessing recent changes in exposure to ALAN in diverse global ecosystem types. This collaboration resulted in a published article (Bennie et al. 2015), which I include in the Appendix 4.

TABLES

Table 1. Studies on macroecology of plants. Number of articles published considering macroecology and vascular plants on the string search (see string search details in Appendix 1).

Kind of studies	No. papers
Direct subject of study	142
Indirect (animal-plant interaction)	22
Indirect (plant-fungi interaction)	4
Indirect (plant-soil interaction)	2
Indirect (scale)	1
Indirect (fire)	1
Mixed taxa	9
Other	87
Total	**268**

FIGURES
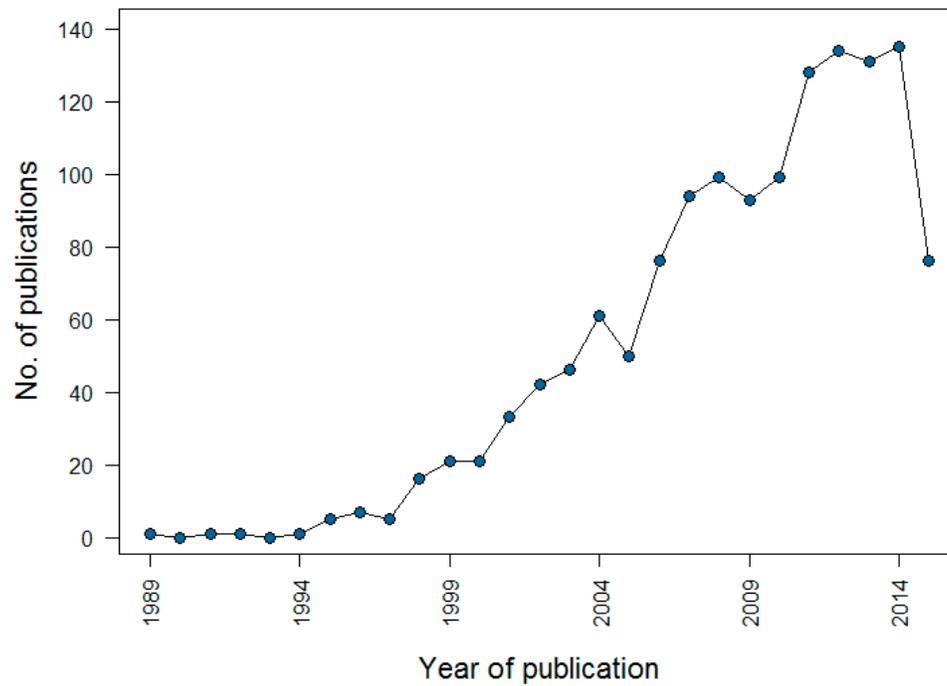
Figure 1. Number of publications per year containing the key word 'macroecology' 1989-2015. The search was conducted in September 2015, so the fall in the graph for this year is due to partial data.
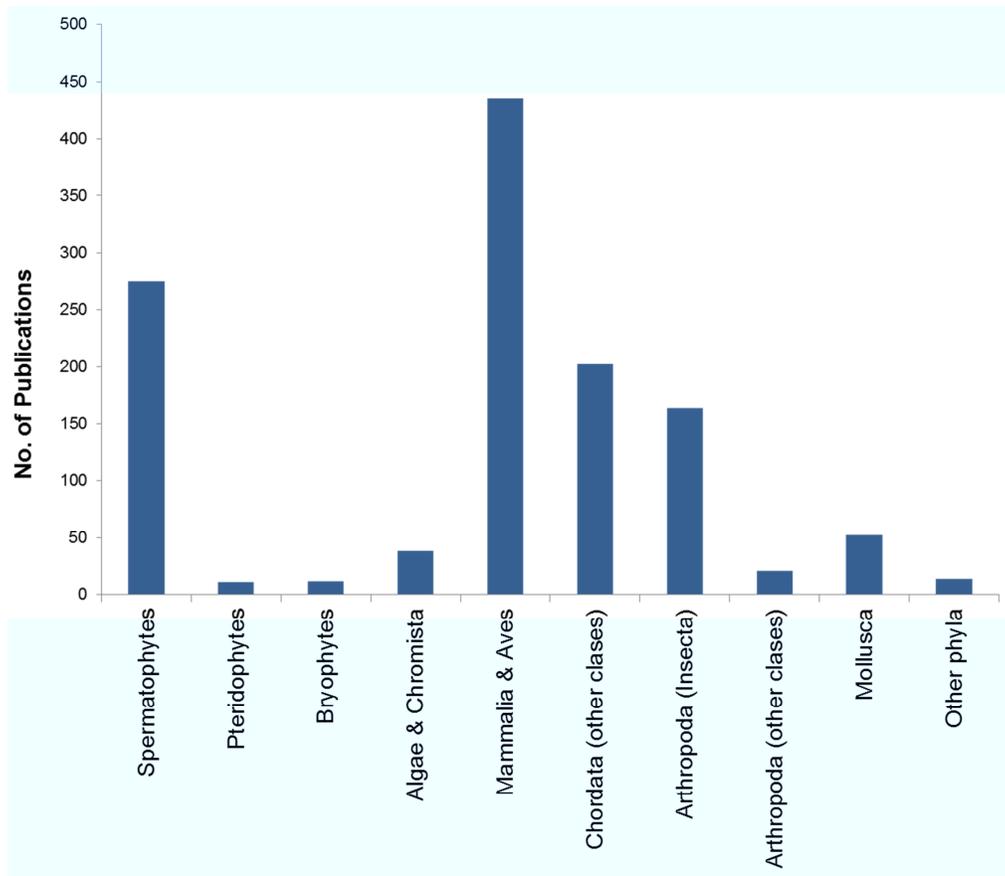
Figure 2. Number of articles published considering macroecology and different taxonomic groups. Results are based on a search on the ISI Web of Science in September 2015 (see Appendix 1 for a search string).
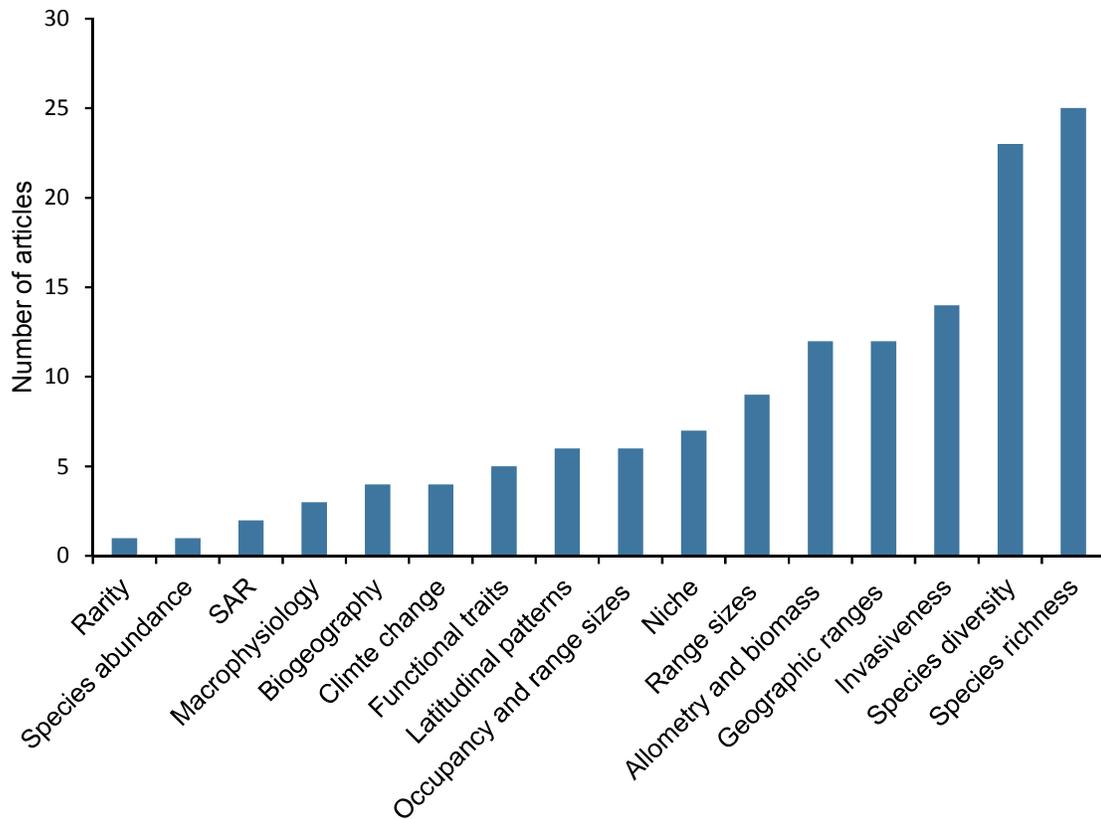
Figure 3. Number of articles published on plant species and diverse topics in macroecology. Note that these topics are general, and some of the articles classified in one category might be addressing two or more of these issues.

CHAPTER 2

Individuals-area relationships are fundamental patterns in macroecology, although less well studied than many others. In this chapter I assess the occurrence of the broad version of these relationships, the generalized individuals-area relationship, which has previously been explored for animals but never for plants.

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INTRASPECIFIC & INTERSPECIFIC INDIVIDUALS-AREA RELATIONSHIPS OF PLANTS

ABSTRACT

Many important patterns and relationships in ecology have been described based on species abundance estimates. There are, however, issues that render these estimates strictly non-comparable across broad ranges of species because of differences in survey methodologies, variations in detectability between species, and the effect of plot area. For animals particular attention has been paid to the relationship between abundance and area through the study of the generalized individuals-area relationship (GIAR), which describes the relationship between the abundance of a species and the size of the plot area where those abundances were estimated. Here, we analyse for the first time the form that this relationship takes for plant species. We used linear mixed effects models and linear models to describe the interspecific and intraspecific individuals-area relationships across 230 plant species, including assessment of the effect of environmental variables, geographic location and human activities. We found that the interspecific individuals-area relationship between plot size and number of individuals, similar to animal species, is less than proportional, even after controlling for putative covariates (e.g. latitude, rainfall, human activities). Abundances spanning a range of plot sizes (≥5ha) were only available for 15 of 230 species, limiting our capacity to characterise variation in intraspecific GIARs. However, for 6 species significant relationships were observed with all having scaling coefficients less than one. The existence of a less than proportionate increase of plant abundances with plot area in the present data set would suggest that caution needs to be exercised in using

compilations of abundances for plant species in testing macroecological theory where these estimates are drawn from plots of different sizes.

INTRODUCTION

The distribution and abundance of species, and the interactions between the two, are fundamental foci of ecological research (Begon et al. 1986, Gaston 2003). Indeed, abundance estimates have now been made for a vast array of organisms in a multitude of places and at many different times (Blackburn & Gaston 1999). Conducting these estimates in such a way as to render them strictly comparable constitutes a huge challenge that remains poorly met, and arguably always will. There are multiple reasons for this, including spatial, temporal and interspecific variations in the detectability of individuals, variation in the suitability and reliability of different survey methodologies, and variation in the abilities of different surveyors (Elton 1932, Haila 1988, Blackburn & Gaston1998, Cassey & McArdle 1999, Southwood & Henderson 2000, Gu & Swihart 2004, Chen et al. 2009, Guarino et al. 2012). In macroecological studies these complications are commonly ignored, on the grounds that underlying patterns in abundance are sufficiently robust, and that they concern sufficiently marked differences in density or population size, that they will nonetheless be detectable. In many instances this may well be true. However, variation in study plot areas, those over which abundances are estimated, has repeatedly emerged as having a systematic effect on abundance estimates that cannot readily be ignored, with the potential to generate spurious macroecological patterns (Blackburn & Gaston 1999).

Two distinct broad relationships between abundances and plot area have been distinguished (Gaston & Matter 2002). The patch individuals-area relationship (PIAR) describes the relationship between the abundance of a species and the size of discrete/distinct habitat patches. Typically, but not invariably, this takes the form of a positive relationship between density and study plot area (Southwood & Henderson 2000, Gaston & Matter 2002, Connor et al. 2000). The second relationship, between abundance and the sampling area designated to characterise abundance is a more general one, and indeed has been termed the generalized individuals-area relationship (GIAR; Gaston & Matter 2002). Here abundance estimates are not necessarily or typically limited to discrete habitat patches, but may derive from more generic study plots or ones where the positioning of the plot with regard to habitat patches is unknown or not of primary interest. In general, this takes the form of a negative relationship between density and study plot area (Pautasso & Gaston 2006), and it is GIARs that form the focus of the present study. Three different kinds of GIARs have been reported. These are (i) intraspecific, where abundance estimates of a given taxon are characterised across a range of study plot areas and the relationship between abundance and plot size for the taxon in question is derived (e.g. Smallwood & Schonewald 1996); (ii) interspecific, where abundance estimates of a range of different taxa typically belonging to a clade (e.g. Aves) are estimated across a range of study plot areas, and the relationship between abundance and plot size is derived across species, with each species represented by one (or sometimes more) data points (e.g. Smallwood 1999); and (iii) assemblage, where the total abundances of all taxa in a given study plot area are pooled and the relationship between abundance

and plot size is derived across assemblages (e.g. Pautasso & Gaston 2006, Jimenez 2000).

The existence of GIARs is important because abundance estimates are quite commonly compiled from the published literature and other disparate sources for the purposes of conducting macroecological (and other) studies (intraspecific, interspecific and assemblage). In most cases no attention is paid to any variation in the areas of the study plots from which these abundance estimates have been obtained, and often these data may themselves not be readily obtainable or indeed documented at all. The conclusions reached may be seriously misleading, including highly inaccurate estimates of population sizes and of the parameters of macroecological patterns (e.g. Smallwood 1997, Gaston et al. 1999).

The principal mechanisms that have been proposed to produce any type of GIARs (intraspecific, interspecific and assemblage) are plot area choice, survey efficiency, habitat heterogeneity and plot edge effects (Gaston & Matter 2002, Pautasso & Gaston 2006). First, GIARs may result from plot area choice if small study plots tend to be less randomly distributed with respect to the density variation of a species than larger plots. This tends commonly to be the case when researchers are concerned to ensure that plots do not entirely miss the species of interest or that a sufficient number of individuals are included (Gaston et al. 1999, Smallwood &, Erickson 1995, Smallwood 2001, Engstrom & James 1981, Blackburn & Gaston 1996, Wiens 1989, Zimmermann et al. 2013). Second, variation in survey efficiency may give rise to GIARs, because there is commonly less likelihood of missing individuals of a species in smaller plots than in larger ones (Borregaard & Rahbek 2010). Third, it has been

proposed that habitat heterogeneity effects might give rise to GIARs, as a consequence of the combination of small plots only being used in density collations when the species of concern is present and small plots having lower habitat heterogeneity (at a given spatial resolution) than do larger plots. In common with the previous mechanisms described, this might be a consequence of the survey methodology (Gaston et al. 1999). Finally, plot edge effects have been proposed to give rise to GIARs. This does not refer to the effect resultant from systematic environmental changes at the edges of study plots (although these may occur when these plots coincide with the bounds of actual habitat patches) but rather the effect of the study plot boundary (Pautasso & Gaston 2006). Smaller areas have a higher ratio of area at small distances from the study plot edge to the total area, compared to large plot areas. This may inflate estimated animal abundances in small plots if surveys include individuals temporarily inside the plot but normally obtaining some or all of their resources from outside.

To date, to our knowledge, all published studies that have sought to determine the existence or otherwise of GIARs, and that have drawn empirical conclusions as to their consequences (see above) have been for animal species. Here we determine, for the first time, how the number of individuals of plant species changes with plot area, focussing on intraspecific and interspecific GIARs (our data were not sufficient also to explore assemblage relationships). In addition, and beyond what has been undertaken for animal GIARs, we also explore these relationships after controlling for human influence, geographic location and a suite of environmental variables.

METHODS

Data

We searched the published literature for studies containing data on the number of plant individuals of a given species recorded in a plot of defined size, and likewise in studies referenced within these papers. Using the ISI Web of Science and SCOPUS we obtained papers using systematic keyword searches (plant abundance, occupancy, plant community diversity, species-abundance distribution, species-area relationship, floristic composition, structure of vegetation, plant density, biodiversity, plant species richness and density or abundance). We also searched systematically through the following journals: Journal of Ecology, Journal of Vegetation Science, and Forest Ecology and Management. Finally, we obtained the Alwyn H. Gentry forest transects data set and the Campbell Webb tree plots data set from Gunung Palung, Indonesia (see Appendix 2 for sources of plant abundance estimated analysed).

Throughout, we focussed exclusively on numbers of individuals (only adults), and did not consider information about, for example, percentage cover or biomass, nor any sources that did not provide data on plot sizes. If surveys were repeated in the same location during different years we used the total numbers of adults counted during the first year of the study only. Demographic studies without independent density data per year and/or for different plot sizes were ignored. The names of plant species were standardized using the Missouri Botanical Garden Herbarium database (APG III System, http://www.tropicos.org/), Kew Botanical Gardens Catalogue (http://apps.kew.org/herbcat/navigator.do) and the Plant List web page (http://www.theplantlist.org/). The initial dataset contained 4,374 records from

40 articles and 4 databases. We then excluded data for species recorded in less than three localities. The final data set thus contained 1,206 records, with plots spanning a latitudinal range between 23.37 South (Brazil) and 47.50º North (Switzerland). See Figure 1. We recorded data about location and where available, growth form, and human activities related to the study site. With regard to human activities, we divided sites into two broad categories: disturbed and undisturbed. These categories were determined based on the information given by each individual publication, where disturbed is considered as a site where human activities were carried out at the moment of the data collection (e.g. logging, selective collection of species, semi-natural managements). An undisturbed site was determined as such when the authors stated that the location of collection was carried out inside a protected area. This information was further verified using bibliography based on the location on the data collection. When data about human activities were not available, but the plant species were collected in a natural protected area, we scored the site as undisturbed. Data on rainfall and temperature for each study site were obtained from WorldClim Global Climate Data (http://www.worldclim.org/current). We selected the annual mean temperature (BIO1) and annual precipitation (BIO12). The extended methodology of how these variables were calculated can be found in (Hijmans et al. 2005).

Plant species abundance

GIARs are commonly expressed as, and discussed in terms of, relationships between the density of a species and the area of each study plot. This, however, raises the potential for spurious negative correlations because plot

area is a component of density which is defined as the number of individuals/plot area which is, in other words, a regression with non-independent variables against each other (Gaston & Matter 2002, Brett 2004). To avoid this problem we focus directly on the relationship between number of individuals and plot area, i.e. between abundance and plot area. A negative relationship between density and plot area implies that the number of individuals measured in a plot increases less than proportionally with the area of the plot.

Statistical analysis

Interspecific relationships. All the analyses were performed using R (2015). In order to describe the interspecific GIAR for plants and to assess the effect of environmental variables, growth form, geographic location and human activities on the number of individuals we used linear mixed effects models implemented in the 'lmer' function of the lmer4 package (Kuznetsova et al. 2014). We used a mixed effects model because we have hierarchical data, i.e. multiple abundance for each taxon nested within the broader overall relationship, meaning that abundances were not all independent of one another (an assumption of OLS regression). In addition, we calculated F and p-values using Satterthwaite approximations to determine denominator degrees of freedom using the lmerTest package (Kuznetsova et al. 2014, Satterthwaite 1946).

We included the number of individuals (log-transformed) as the response variable and plot size (log-transformed), latitude, longitude, rainfall, temperature, growth form (with four levels: herbaceous, liana, shrub and tree), human influences (with two levels, disturbed and undisturbed) as additive fixed factors. We also included the interaction between growth form and plot size

because growth form can have an influence on the size of the plot (e.g. relatively larger plots are needed to study tree abundance, whilst herb abundance can be studied in relatively smaller plot areas). In addition, the number of individuals is likely to be affected by a number of factors; hence we incorporated latitude, longitude, rainfall and temperature to ensure that our results were not confounded by these. We included a random intercept at the level of species, which modelled variation in abundance among species driven by other unmeasured variables and allowed us to control for non-independence of the residuals. Also, we introduced biome (Olson et al. 2001, data access through WWF, 2014 (www.worldwildlife.org)) and island in the random effect structure. Biome was added to control for a bias in the coverage of the data set towards particular regions of the world. Island was added to control for the possible effect of density compensation, where the densities of island species are greater because of a lower species richness compared with mainland species (MacArthur et al. 1972). We fitted the most complex model (e.g. with all additive terms and the interaction between plot area and growth form) using maximum likelihood and then followed a backward stepwise strategy for model selection by elimination of non-significant terms using the 'step' command implemented in the 'lmerTest' library. Elimination of the non-significant fixed effects is done one at a time following the principle of marginality: the highest order interactions are tested first; if they are significant, the lower order effects are not tested for significance (Kuznetsova et al. 2014). The automatic elimination of terms implemented by the 'step' command considers the Satterthwaite degrees of freedom calculation, since we are testing on the boundary (Zuur et al. 2009). We ignored numbers of individuals recorded in plot areas smaller than 0.1ha, because initial model checks revealed these to be

outliers. The final model was refit using restricted maximum likelihood to obtain the parameter estimates. We used a likelihood ratio test to compare differences between the final model and a separate model that included exclusively plot size as a fixed factor. The random structure for the separate model remained as in the final model. Deviance explained by the different models was calculated by comparing the deviance to a null (intercept only) model such that *% deviance = (deviance$_{null}$-deviance$_{model}$) / deviance$_{null}$*. In addition, we used AIC values to determine the most parsimonious model. Temperature, rainfall and latitude were evaluated for collinearity using variance inflation factors (VIFs) implemented in the package 'car' (Jon et al. 2014). VIF values for pair-to-pair comparison between variables showed latitude and temperature with values of 5.8 as the higher correlation estimates (Table A2.2.1, Appendix 2). The resultant VIF value was not large enough (VIF≥10) to drop any variables from the general model (Estrada-Peña et al. 2013).

Intraspecific relationships. The sample size of data at the intraspecific level was poor; most species were measured over a very narrow range of plot sizes and had relatively few abundance entries. To get a clear idea of intraspecific individuals-area relationships, an individual species must be measured over a reasonable range of plot sizes. We considered species recorded on plot size ranges of ≥5ha to have a sufficiently large range to derive an intraspecific relationship. We analysed intraspecific individuals-area relationships by using OLS regressions on each species. The slopes of the intraspecific relationships were evaluated using model outputs of two-tailed t-tests comparing the slope coefficient to a slope of zero, with $p < 0.05$ indicating significance.

RESULTS

The final data set analysed contained 1,281 records, i.e. each record represents one abundance value for a species. From these, we obtained 33 different plot areas belonging to 230 species with at least three records per species. Plot size ranged from 0.1 to 216ha. The average plot size was 4.6ha and the median was 2ha. 1207 records were recorded in plots with areas ranging from 0.1 to 10ha and 74 from plots between 11 and 216ha.

Interspecific individuals-area relationship. The final model obtained included plot size and rainfall amongst the fixed effects and species and biomes for the random effects (Table1). The slope of this interspecific GIAR, after controlling for the above covariates, was 0.38 (95% C.I.: 0.0.32 to 0.46), which indicates that the number of individuals increased less than proportionally with plot area (Figure 2). Thus, density declined as a function of plot area. The model including plot size and rainfall explained a marginally higher percentage of variation than the plot size only model (58% and 57.97 respectively). The plot size and rainfall model was also slightly more parsimonious with a lower AIC value (1898.7 vs. 1901.2 correspondingly), giving little support to rainfall as the difference between AIC is <3

Growth form and its interaction with plot size, together with human activities and the geographic coordinates were not significant in explaining the number of recorded individuals (see Appendix 2.3 for p-values of non-significant terms).

Intraspecific individuals-area relationship. From the 15 species with plot size ranges of five hectares or larger, six had significant relationships between number of individuals and plot size with slope values shallower than one, i.e.

increasing less than proportionally (Table 2 & Figure 3). For the other nine species no significant relationship was obtained (Table 3 & Figure 3).

DISCUSSION

In this study we test for the first time the existence of GIARs for plants. In common with animals, we found that the number of individuals of plant species increases less than proportionately with area, i.e. there is a negative interspecific relationship between the density of individuals and plot area. The relationship persisted even when controlling for a variety of potentially confounding factors, a form of analysis that has not previously been conducted in this context, although the converse approach of controlling for plot area in order to understand the role of other factors has been employed (e.g. Pautasso & Gaston 2006).

Interspecific GIARs may arise in two ways. They may be a consequence of the aggregation of multiple negative intraspecific GIARs (increase of number of individuals less than proportionate with area), or they may be driven by species that occur at lower densities being sampled, intentionally or otherwise, using larger plot sizes. The first of these is not a sufficient condition for GIARs to arise, as intraspecific GIARs could be consistently negative without leading to a negative interspecific GIAR, and a negative interspecific GIAR does not necessitate negative intraspecific GIARs, therefore the relative contribution of the two processes may be variable. The most frequently cited reason for expecting negative interspecific GIARs, whether negative intraspecific GIARs occur or not, is that larger plot sizes tend to be employed for assessing the abundances of larger bodied species, which tend to have lower densities where

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they occur (Village 1984, Schonewald-Cox et al. 1991, Blackburn & Gaston 1996, Blackburn & Gaston 1997). This is plainly the case for animals (e.g. the abundances of mice are typically measured on trapping grids of the order of tens of metres in extent, and the abundances of elephants on the scale of national parks). Even though it tends also to be the case for plants, with herbs being studied on smaller plots than trees (as a rule of thumb the study of grass species is carried out in plots of $0.1m^2$, while tree species are studied in transects of at least $10m^2$) evidence for this mechanism was not detected in our plant data set. The non-significant interaction between growth form and plot size in the linear model is an indication that interspecific GIARs might not be achieved by the choice of plot sizes being influenced by plant sizes. Even when plot sizes in the study of plant species change with regard to the size of the plant and/or whether a study is focussed on cover or on plant numbers per unit area, the range of plot sizes is traditionally not as broad as in animal studies (Usher 1975, Chytrý & Otýpková 2003, Kéry 2004) maybe due to the probable standardisation of plot sizes since Greig-Smith (1952).

Despite the limitation in the range of plot areas and the low number of records per species (that may limit the probability to find a significant relationship, see Figure 3), intraspecific GIARs are occurring amongst 40% of the plant species tested. For animal species, intraspecific GIARs seem likely often to result simply as a consequence of plot area choice. Such effects seem no less likely to occur for plants than for animals, but the range of variation in plot sizes used for the former tends to be substantially less than for the latter; data on abundance and density estimates have been published for many animal species that are derived from plots that vary in area by several orders of magnitude (e.g. in studies of kestrels, study areas range from 1 to 16,000 km^2,

Village 1984) and this does not happen in our data set for plants (which lacks the very large plot sizes commonly employed in animal studies). This may result in a lower occurrence of intraspecific GIARs for plants than for animals. The effect of the variation in survey efficiency with plot area may be reduced for plants compared with animals because of the smaller range of plot sizes that are employed, and because individual plants cannot respond to the presence of an observer by hiding or departing a survey plot. Despite the sessile nature of plants, some authors have argued that there are important sources of heterogeneous detectability during field work, including differences in morphology or life-form and the observer effect (Chen et al. 2009, Kéry et al. 2006). The imperfect detection of individuals of plant species, i.e. the bias from the observer, may lead to intraspecific GIARs although this might be less frequent for plants than for animals. Habitat heterogeneity seems likely to influence plants and animals equally, although it will also be sensitive to differences in the range of plot sizes. Plot edge effects can inflate estimated animal abundances if, for example, individuals counted inside the surveyed plots were there momentarily, but used to be outside. This mechanism is plainly not applicable in plant surveys, although there remain issues of what to do when the entirety of an individual does not lie within a survey plot. In sum, plot area choice, survey efficiency and habitat heterogeneity all appear to be plausible mechanisms for the production of intraspecific GIARs in plants as well as animal species.

The paucity of intraspecific GIARs for plants means that there is a lessening of any parallels to the concerns that have arisen around using compilations of density estimates for animals in macroecological studies without paying close attention to (and often analytically controlling for) the plot areas

from which these are drawn (Gaston et al. 1999, Kéry et al. 2006). Attention may, nonetheless, need to be paid to this issue if the range of plot sizes employed to assess the abundances of individual plant species grew, as might occur for example with developments in the potential for identifying individuals and species using remote sensing imagery (e.g. Foody et al. 2005, Verbug et al. 2011, Crowther et al. 2015).

If indicative of a more general pattern, the existence of a negative interspecific GIAR for plants in the present data set would suggest that caution needs to be exercised in using compilations of abundance estimates for plants in testing macroecological theory, for example, where these estimates are drawn from plots of different sizes or when they are not considered at all during analysis (e.g. Crowther et al 2015). Particular concerns arise in this regard given the potential inflated statistical significance of using the scaling exponents for macroecological relationships as part of the evidence base for differentiating amongst competing mechanisms, and the challenges this already poses given the inevitable 'noise' in ecological data.

TABLES

Table 1. Fixed effects estimates of the final model fitted with REML.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.066	0.0962	11.08	<0.001***
Log10(Plot size)	0.386	0.035	10.87	<0.001***
Rainfall (mm, annual mean)	-0.00006	0.0000	-2.17	0.03*

Signif. codes: 0 '***' 0.001 '**' 0.01 '*'

Table 2. Summary information for the six species that showed a significant intraspecific individuals-area relationship.

Species	Coefficient (slope value)	CI		Std. Error	t-value	p-value
		Lower	Upper			
Anacardium excelsum	0.42	0.05	0.80	0.18	2.27	0.02
Apeiba tibourbou	0.31	0.2	0.4	0.18	1.6	0.11
Astronium graveolens	0.42	0.06	0.79	0.18	2.3	0.02
Garcinia intermedia	0.84	0.46	1.22	0.19	4.43	<0.001
Gentiana cruciata	0.62	0.40	0.84	0.11	5.61	<0.001
Simarouba amara	0.74	0.46	1.03	0.14	5.2	<0.001

Table 3. Summary information for the nine species that showed non- significant intraspecific individuals-area relationships (p-value >0.05).

Species	Coefficient (slope value)	CI		Std. Error	t-value	p-value
		Lower	Upper			
Brosimum alicastrum	0.4	-0.08	0.8	0.21	1.9	0.1
Cecropia insignis	-0.1	-2.34	2.5	0.99	-0.1	0.9
Hieronyma alchorneoides	0.5	-1.3	2.3	0.3	1.6	0.1
Laetia procera	0.21	-0.2	0.6	0.2	1.12	0.2
Paullinia pinnata	-1.5	-4.24	1.2	0.75	-2.04	0.05
Scaphium borneensis	-1.4	-15.1	12.2	2.1	-0.71	0.5
Shorea parvifolia	0.5	-0.5	1.3	0.5	0.9	0.3
Terminalia amazonia	0.4	-0.83	1.6	0.22	1.7	0.09
Ximenia americana	0.6	-1	2	0.3	2.03	0.05

FIGURES
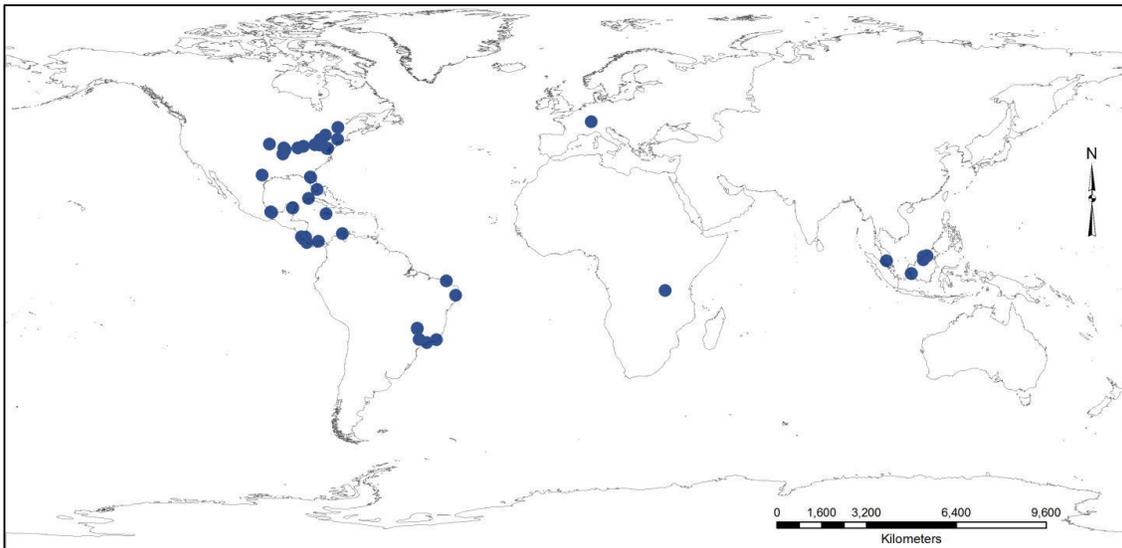
Figure 1. Global distribution of the data for species recorded in less than three localities.
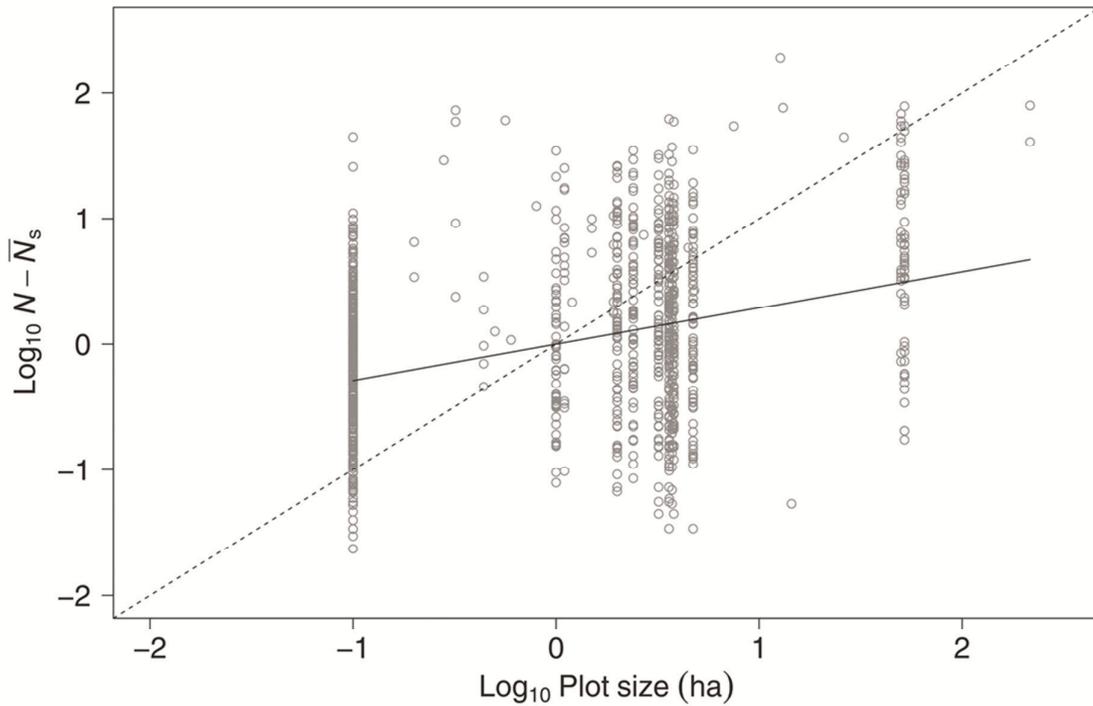
Figure 2. Interspecific individuals-area relationship for plants. The response variable was standardised by subtracting the estimates (on the intercept) from the linear mixed effects model (by using the final model (log10(number of individuals)=1.066 + 0.38(log10(plot size ha) -0.00006(mm) + random) refit with restricted maximum likelihood to the number of individuals of each species). Analysis shows that the number of individuals increases with a less than proportionate; slope value= 0.38, 95% CI: 0.32 to 0.45. Dotted line represents a slope of one. Each dot represents an abundance entry on the data set.
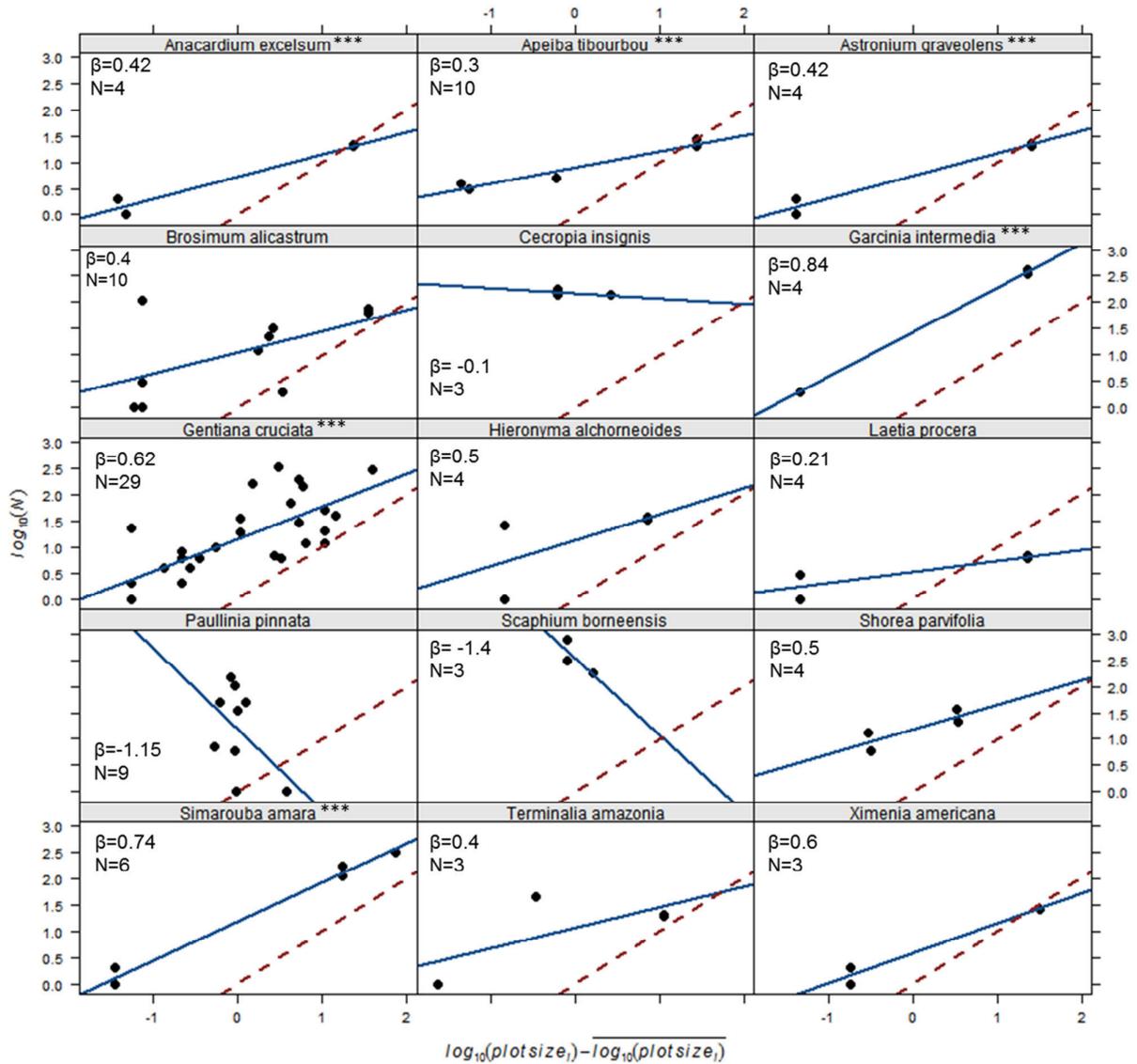
Figure 3. Intraspecific-individual relationships for the 15 species with plot sizes ranges ≥ 5ha. The explanatory variable was subject centered for the purpose of depicting all the species together. The response variable is represented by the logarithm (base 10) of the number of individuals. The slope values are represented by β, and the dotted line is the slope of one. *** Significant species (see Table 2).

CHAPTER 3

Continuing the exploration of individuals-area relationships, the third chapter examines a less general pattern: the patch individuals-area relationship. This is distinguished from the generalised individuals-area relationship by considering only abundance estimates of a species from genuine habitat patches, commonly fragmented habitat patches, and the chapter considers the implications for its form and shape of three notable theories in ecology (the equilibrium theory of island biogeography, the resource concentration hypothesis and the density compensation theory).

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Authors' contribution:

Conceived and design: MEC-C, KJG.

Data provision: RA, VAR, TK, FPLM, BM, BAS.

Analysis: MEC-C.

Draft manuscript: MEC-C.

PLANTS AND PATCH INDIVIDUALS-AREA RELATIONSHIPS

ABSTRACT

Three distinct relationships between animal population densities and patch areas have been hypothesised: the equilibrium theory of island biogeography predicts that population density remains constant with increasing area; the resource concentration hypothesis predicts an increase of density with area; and the theory of density compensation predicts a decrease of density with increasing patch area. In this chapter, we explore for the first time the form of this relationship for plant species and analyse its implications for the hypotheses commonly tested for animal species. We used six independent data sets from Brazil, Ethiopia, Kenya and Mexico, to test whether the density of plants is dependent on area in individual species. Our results are consistent with those for animal species, in as much as population densities increased with patch area for many plant species. However, far for being a general result, a high proportion of all species tested did not show evidence of such a relationship between density and patch area (many relationships were negative). This variability between species, and the potential differences of PIARs between animals and plants, may be challenging in determining the implications of variations in patch areas for conservation management of species and assemblages.

INTRODUCTION

The density of a species and the area over which that density is measured have commonly been found to be correlated, with potentially important consequences for the interpretation of density estimates. These relationships fall into two broad categories: generalized individuals-area relationships (GIARs) and patch individuals-area relationships (PIARs; Gaston & Matter 2002). GIARs concern the relationship between the densities of species and the sizes of the areas from which those densities have been determined (e.g. plots, transects), with no particular constraint on the nature of those areas (i.e. they can be quite arbitrarily defined; Gaston & Matter 2002). In general, this relationship tends to be negative, with the density of individuals declining with increasing area (i.e. the number of individuals increases more slowly with increasing area; Pautasso & Gaston 2006), and is principally of concern because of its implications for the comparability of density estimates obtained from different studies, and the consequences for the use of such estimates in macroecological analyses and applied ecological analyses (see Chapter 2).

In contrast, PIARs are concerned with the relationship between the densities of species and the sizes of well-defined habitat patch areas (e.g. natural or artificially created habitat patches in a matrix of alternative habitat; Connor et al. 2000, Gaston & Matter, 2002). Substantial attention has been paid to PIARs for animal species, and most studies have described marked positive relationships (Kareiva 1983, Haila 1983, Connor et al. 2000, Cozzi et al. 2008). However, as with many macroecological patterns, there is considerable variation, and indeed some studies have documented negative PIARs while others have found no simple relationships at all (Nupp & Swihart 1996; Schmid-Holmes & Drickamer 2001; Anderson & Meikle 2006).

Variation in the density of individuals with patch area has important implications both for conservation management (Simberloff & Abele 1982; Hanski 1994; Gaston & Matter 2002) and ecological theory (Connor et al. 2000, Matter 2000), and has thus been explored in a variety of contexts. Research has been stimulated particularly by concerns over the impact of habitat loss and fragmentation on natural systems (Andrén 1994): fragmentation decreases the availability of a focal habitat, and the remnants are often arranged across the landscape as island-like habitat fragments of different sizes (Brotons et al. 2003). Ecological theory, however, provides no consensus as to what form PIARs should take, and hence no expectation of the consequences of the form of habitat fragmentation for the density of individuals. The equilibrium theory of island biogeography (ETIB) of MacArthur and Wilson (1967) assumes that the number of individual organisms in the taxon of a given island, increases linearly with the area of the island (p.13). In other words, the theory assumes that density remains constant with increasing area. The resource concentration hypothesis (Root 1973) predicts that the density of individual species should increase with patch area as a result of a greater concentration of resources in larger areas. Finally, in the density compensation hypothesis (MacArthur et al. 1972) individual species present in both large and small patch areas should have higher densities in the smaller patches as a consequence of lower species richness resulting in reduced interspecific competition (Brotons et al. 2003).

Given the potential implications of PIARs for animal species it is surprising that, to our knowledge, no previous studies have sought to determine their existence and form for plant species. Here we address this issue using an extensive dataset compiled from existing studies which have measured plant species densities in given habitat patches. We explore whether these

relationships are better explained by the equilibrium theory of island biogeography, the resource concentration hypothesis or by the density compensation phenomenon.

METHODS

Data

Analyses were based on five data sets, obtained from studies performed in Brazil (Santos et al. 2008, 2010), Mexico (Arroyo-Rodriguez et al. 2009, Hernández-Ruedas et al. 2014), Ethiopia (Aerts et al. 2006, 2011) and Kenya (Aerts et al. 2010, Thijs et al. 2014). In each case, the habitat patches were well-defined and well-differentiated from the surrounding areas.

Brazil data set. The fragments at Usina Serra Grande belong to the Atlantic Forest of Brazil, and are entirely enclosed by a uniform, stable and inhospitable matrix of sugarcane monoculture (Santos et al. 2010). The vegetation was sampled in plots of 10m by 100m (0.1ha) at the geometric centre of each patch. Diameter at breast height (DBH) at 1.3m of each tree was recorded, and all trees ≥ 10cm DBH were inventoried. Basal areas (BA) were then calculated using the formula $BA=\pi*(DBH/2)^2/1000$, where 1000 is a factor to convert cm^2 to m^2. In total, 20 small forest fragments ranging from 3.4 to 79.6ha (Santos et al. 2010) were sampled.

Mexico data sets. Data sets from Mexico were obtained from two different regions: Los Tuxtlas Biosphere Reserve on the Atlantic Coast and Lacandona rainforest which stretches from southeast Chiapas into northern Guatemala and the Yucatán Peninsula. The patches of rainforest at Los Tuxtlas

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are bounded by a matrix of pasture and cropland (Castillo-Campos & Laborde 2004). The fragments of Lacandona rainforest occur amidst land used for agricultural purposes (Hernández-Ruedas et al. 2014). The collection of plant densities in both regions of Mexico (Los Tuxtlas and Lacandona) was based on Gentry's (1982) sampling protocol. Vegetation was sampled within each patch using randomly located 50m by 2m (0.1ha) plots. All species of trees, palms and shrubs with a diameter at breast height (DBH) ≥ 2.5cm were recorded (Arroyo-Rodriguez et al. 2009). At Los Tuxtlas, 45 randomly selected patches were sampled, ranging from 0.737 to 700ha. At Lacandona, a total of 26 patches ranging between 2 and 90ha were sampled (Hernández-Ruedas et al. 2014).

Ethiopia data set. The Ethiopia data are from two regions: the Geba river watershed in Central Tigray, and southwest Ethiopia near the village of Garuke. Central Tigray patches are remnants of sacred forest and are the only remaining forest patches in the study area of approximately 13000ha, north of the Tsilme and Gereb Aba Haylu rivers, and embedded in cultivation and heavy livestock grazing areas (Aerts et al. 2006). At this location, data collection was performed using a random design and a density of approximately one 20m by 20m (0.04ha) plot per 2ha in each fragment, with 31 plots sampled in total. Within forest fragments, sample plots were located more than 50m apart to ensure independence. Each tree ≥ 1m in height and all multi-stemmed individuals ≥ 2m in height were identified to species level. Shrubs (all single-stemmed <1 m in height and all multi-stemmed individuals < 2m in height) were sampled in a random 10m by 10m subplot within the 0.04ha plot.

The fragments near Garuke are of a semi-forest coffee system, and are surrounded by a mosaic of crop land, pasture, riverine wetland, small human settlements and isolated farmsteads, and patches of exotic timber tree species (Aerts et al. 2011). Data were collected using a two-stage sampling design to select 26 random plots of 20m by 20m (0.04ha), where all woody plants taller than 2m (including palms) were recorded. In total, 20 forest fragments were sampled, which represented the full range of fragment sizes (0.2ha to 33ha) in the area.

Kenya data sets. The fragments of the Taita Hills forest in Kenya are remnants of the Afromontane forest (known also as cloud forest) located in the southeast, 25km west of Voi in the Taita-Teveta District. These patches are surrounded by plantations of exotic species (Aerts et al. 2011). Stem numbers of woody species in the forest patches were sampled in 82 plots of 0.04ha. In total, 12 patches were sampled, ranging from 1ha to 185ha (Thijs et al. 2014).

Data sets from Ethiopia and Kenya include presences and absences of the individuals for all the plant species recorded from the entirety of the surveyed patches. This information is very valuable, given that the vast majority of density estimates for organisms are based only on sites at which a given species actually occurs, ignoring those patches from which it is missing (Gaston 2003). These data sets, thus give the rare opportunity to compare PIARs built only with data from those patches in which a species occurs and those built with data both from patches in which it does and does not occur (see Figure 1 for the location of the study areas).

Most studies consisted of a single field season, so the absence of a rare or less abundant species from some patches is to be expected (McArdle 1990).

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Strictly speaking, the density in patches where no individuals of a particular species were observed in the year of the study is not zero, but some small unobservable value, given the short duration of most studies (Connor et al. 2000). The data set from Ethiopia and Kenya gives us the opportunity of testing whether considering both the occurrences and the absences recorded makes a difference compared with recording occurrences exclusively.

Analysis

All analyses were conducted using R (2015). Analyses were conducted separately on two subsets of the data based on two criteria: 1) on the differences in survey methodology, i.e. based on the size of the plot used to record plant numbers, and 2) on whether just presence in plots or both presence in plots and presence and absence of species for patches were recorded. Subset 1 includes the data from Mexico and Brazil, with data recorded on plot sizes of 0.1ha. Subset 2 includes data from Ethiopia and Kenya, with data recorded on plot sizes of 0.04ha and with presence-absence information for each entire patch. Density estimates were calculated by dividing the number of individuals by the plot size (ha) for both subsets, however, the analysis was restricted to species recorded on five or more patches for subset 1 to account for variability in the range of patch sizes.

For subset 2 we restricted the analysis to species recorded on five or more patches when we excluded zero patches, i.e. by considering absences of species from the patches, but we considered all species for the analysis that includes zero patches (occurrences and absences).

Hypothesis tests

The equilibrium theory of island biogeography (ETIB). This theory assumes that species densities remain constant with, patch area. In other words, we expect to obtain a slope between species density and patch area not significantly different from zero; note that the statistical non-independence problem highlighted in chapter 2 does not apply here because we are using species densities from plots and areas for the entirety of the patches in which those plots are nested. We tested this mechanism first on individual species. A log-log regression model was applied to all species for subset 1 (following the typical interpretation of the equilibrium theory of island biogeography and for analytical convenience, to linearly fit the data). The slope of the regressions was considered as a measure of the effect of patch area on plant density estimates, and p-values and R-squared values were considered as estimates of the significance and fit of the models, respectively.

The resource concentration hypothesis. This theory states that individual animal species generally display higher population densities in larger patch areas (Root 1973). If such a relationship occurs for plant species, we would expect to obtain a positive relationship between densities and patch area. Equally, plant biomass could still increase with area (providing greater resources for, say, animals) due to a potentially higher concentration of resources in larger patches, and the differential allocation of such resources, ,but this need not be reflected in plant density. As a test of the resource concentration hypothesis we thus analysed both densities and basal area of tree species in Brazil, in relation to patch area. In order to describe the

individual basal area-patch area relationship we used an OLS regression between each individual tree basal area and patch size, both log-transformed.

Density compensation. Density compensation theory states that the summed population density of individuals of all species on an island is equal to the summed mainland density (MacArthur et al. 1972). This phenomenon is based on the observation that the occurrence of fewer species on islands leads them to have higher population densities than do species on the mainland. These increased densities on islands have been explained as a consequence of species on islands experiencing less competition than on the mainland (MacArthur et al. 1972, Cody 1974). However, Williamson (1981) and Schoener (1986; see Connor et al. 2000) proposed that if the total number of species is independent of island size (as assumed by the ETIB) and if a species-area relationship exists, there is no need to infer competitive release to account for density compensation. Irrespective, if this applies to our habitat fragments, with smaller patches behaving more like islands and larger ones more like mainland (as suggested by MacArthur & Wilson 1967), or both smaller and larger patches as islands of different sizes (MacArthur & Wilson 1967) we expect to observe a decrease in the average density of all species present with the increase of patch area. This hypothesis was tested with subset 1, by adding densities of all species occurring at a given patch and by considering each species separately at different locations.

Zero patches. PIARs have almost invariably been reported based on density estimates from part of the habitat patch, given the logistic challenges of exhaustive surveys of entire patches, on the assumption that this is representative of the whole, and ignoring patches from which a given species

was unrecorded, often because data on whether such absences pertained to the whole patch were not available. The inclusion or exclusion of such zeroes could, however, have a substantive effect on the form of the PIAR that is documented. Evidence suggests that positive patch density-area relationships for animal species might be obtained due to small patches having zero densities (Loman, 1991; Bowers & Matter, 1997). To assess this effect we used models both excluding (as elsewhere in the analyses) and including patches with sampling zero densities (where the species is absent from the plot but present in the patch) using data from subset 2.Similar to subset 1, we first applied a log-log regression model to each individual species. We added one (n+1) to the number of individuals to be able to log-transform data when including absences. When zero patches were considered in the models, all species were included, as all of them have occurrences and absences reported for all the range of patch areas. However, we selected species recorded in five or more patches only (to account for variability in the range of patch sizes) to perform the linear regressions when zero patches were excluded.

RESULTS

We analysed 3,791 records of 291 species from subset 1 (plot size = 0.1ha) recorded in at least five different patches. The smallest and the largest patch area for this subset were recorded at Los Tuxtlas, Mexico (0.737 and 700ha). For subset 2 (plot size = 0.04ha) we analysed 1,917 records of 137 species that occurred in one or more patches. The smallest patch was documented at Garuke, Ethiopia, in the semi-forest coffee system (0.22ha) and the largest was

recorded at Taita Hills in Kenya (185ha). Most of the records were from patches with areas of less than 100ha for both subsets of data (Figure 2).

Hypothesis tests

Of 291 species from subset 1, 92.4% showed significant patch density-area relationships. 153 plant species (53%) showed a significant negative relationship (p-values ≤0.05) with slope values ranging from -1.04 to -0.0003. 112 species (38.5%) showed a significant positive relationship between density and patch area with slope values ranging from <0.0001 to 0.6 across locations (Table 1, Figures 3 & 4). For four species, the number of individuals did not differ systematically across patches of different sizes (*Aspidosperma megalocarpon* Muell. Arg., *Ficus colubrinae* Standl., *Ficus oerstediana* (Miq.) Miq. and *Parathesis lenticellata* Lundell. There was no support for any individuals-patch area relationship for 7.6% of the plant species analysed.

The relationship between the biomass of individual species and patch area showed that, for all the 31 species analysed there were significant positive individual biomass-patch area relationships (p-values≤0.05), although with very shallow slope values, ranging from 0.002 to 0.005 and R^2 > 0.9.

The supplementary test for density compensation from subset 1, found no significant relationship between overall mean densities (averaged across species) and patch area for any of the data sets (b.Lacandona= -0.03, C.I.: 95%: -0.133 to 0.08; b.Tuxtlas = 0.009, C.I.: 95%: -0.045 to 0.065 and b.Usina = -0.1, C.I.: 95%: -0.23 to 0.05, Figure 5).

137 different species were analysed considering zero patches. Overall, 115 species (84%) showed significant negative PIARs, and 35 significant positive PIARs (p-values≤0.05, Table 2, Figures 6 & 7). 44 species with significant negative relationships had an $R^2>0.5$, whilst only 3 species with significant positive relationships had an $R^2>0.5$. Excluding zero patches from the analysis, 37 species were present in 5 or more patches across the different locations (Table 2, Figures 6 & 7). From this, 30 species (81%) showed significant negative relationships, with 9 of them showing $R^2>0.5$. Only 4 species showed significant positive PIARs.

DISCUSSION

We have examined for the first time the existence of the patch individuals-area relationship for plant species and the possible mechanisms. At the intraspecific level, focusing on subset 1 of the data, 53% of the species exhibited statistically significant negative PIARs, with a somewhat lower percentage having statistically significant positive one (and a small percentage having non-significant relationships; Table 1). This suggests that the prevalence of positive PIARs that has been documented for animal species is not also found for plant species, although the breadth of data sets that have been examined for animal species is much wider than those analysed here.

The data sets that have been studied for animals also have other characteristics that are not especially well replicated in the plant analysis we report. Bowers and Matter (1997), for example, argue that significant positive PIARs for animal species are most commonly found when a larger range of patch areas and a greater number of patches are included in the analysis. Our

data sets, which were nonetheless costly to obtain in terms of resources and effort, are rather limited in the overall range of patch sizes, and many species only occur in a relatively small number of those patches. That said, our plant data sets comprise markedly more species than is typical of those that have been analysed for animals, and thus provide rather more insight into the relative frequencies of positive and negative PIARs than has previously been possible within individual data sets.

The positive PIARs commonly observed for animal species have been argued to be consistent with the resource concentration hypothesis, with larger patches containing higher densities of resources enabling higher densities of those species exploiting them to be maintained (Connor et al. 2000). Quite what is meant by resources in the context of those studies, and why their densities should be higher, is often rather vague. Sometimes it appears that the expectation is that the densities of predators are thought to be higher in larger patches because the densities of herbivores are higher, and the densities of herbivores are interpreted to be higher because the same pattern is assumed for the plants on which they feed. This last step has been tested predominantly under experimental conditions, which have not found consistent results. Indeed, some studies have found positive density-patch area relationships (Connor et al. 2000, Lancaster & Downes 2004), others a negative relationship (Bach 1988), no relationship at all (Grez & González 1995) or a mix between the last two forms (Cromartie 1975, Kareiva 1985, Bender et al. 1998, Hambäck & Englund 2005). The pattern of slopes of PIARs documented here provides no consistent support for the resource concentration hypothesis, as most of the PIARs were negative. However, our test for the resource concentration hypothesis considering biomass (as explained in the introduction, given the

often great intraspecific variation in size for plants a higher concentration of resources in larger patches could lead to a higher biomass of a species, rather than a greater density), albeit limited, leads indeed to a significant positive increase of biomass with patch area for the species tested. Some positive PIARs for plant species might be a result of the concentration of resources on larger patch areas, but a test considering biomass is necessary rather than a test considering densities. A plausible explanation sustaining the existence of the resource concentration hypothesis for plants is that higher availability of resources in larger areas might lead to individuals of trees species to differentially allocate biomass, such that an increment in the tree basal area can be observed with larger patches. As we tested this hypothesis for species recorded in the geometric center of the patches, i.e. the plant species considered here are likely to be forest-interior shade-tolerant and large-seeded species, with large trunks, supra-annual reproduction, and specialised pollination systems (Laurence et al. 2006, Lopes et al. 2009, Tabarelli et al. 2010, Arroyo-Rodríguez et al. 2013), we expect that larger areas are more suitable for them, which might be reflected in an increase of biomass allocation with area. This idea is supported by the fact that in smaller patches edge effects trigger a degeneration process, in which plant communities will retain gradually fewer species and lower biomass over time (Whitmore 1989, Santos et al. 2008, 2010).

Amongst animal species, negative PIARs have been interpreted as a consequence of density compensation, in which the lower species richness associated with smaller patches enables those that are present to attain higher densities. This assumes that the summed densities of species are approximately constant across patches of different sizes, and that the mean

density across species declines as patch size gets larger. Whilst a high proportion of intraspecific PIARs in our data sets are negative, we found no evidence of this last pattern, with there being no significant relationship between the mean density across species and patch size. This makes sense given the heterogeneity of PIARs that we have documented, which would tend to undermine the likelihood of any systematic change in the average density of individuals across species with changes in patch size. One might also anticipate differences between plant and animal species in this regard, because of the typically greater potential for the former to persist in patches for long periods as even single individuals (especially for trees).

Concern has been expressed that negative PIARs for animal species may be a consequence of a decline in the efficiency of sampling with increasing patch size, such that individuals are more likely to be missed and densities more markedly underestimated in large patches than small ones (see also Chapter 2). This seems unlikely to be the case in our data sets. The plot based approaches to estimating densities employed mean that densities are estimated over the same sized areas regardless of the patch size, and the sampling within those plots is exhaustive, or a close approximation. These approaches may potentially bias the density estimates of some kinds of species, 'edge' species for example, but probably provide more reliable data than has previously commonly been used in studying PIARs.

Almost invariably, zero density estimates of a given species have been excluded from analyses of the form of its PIAR in a particular data set (e.g. Connor et al. 2000). This may be logical, in as far as concerns often prevail as to the difficulty of distinguishing absences that are driven by population dynamic

processes (the focus of interest around PIARs) and by habitat suitability, and the complete exclusion of zero density estimates avoids any need to try to differentiate between the two. However, the question remains as to what impact the exclusion of zero density estimates may be having. Unusually, two of our data sets provided the opportunity to distinguish between, at the patch scale, sampling zeros (the absence of a species from a sampling plot that was actually present on the patch in which the plot occurred) and genuine zeros (the absence of a species from a sampling plot and the patch in which the plot occurred) (Wright, 1991, Bowers & Matter 1997, Connor et al. 2000). However, this made little difference to the overall patterns observed, with most species having negative PIARs in both cases.

Combining the findings of this chapter with those of chapter 2 suggests that individuals-area relationships of any form (GIAR or PIAR) are much less consistently prevalent and consistent in direction for plants than they are for animals. In some ways this suggests that the concerns that these relationships have given rise to for the handling of density data for animals are much less acute for plants. Equally, and particularly in the context of PIARs, it suggests that recommendations as to the implications of habitat fragmentation, as to the appropriate management responses, may be much harder to make for plants than animals.

TABLES

Table 1. Significant slopes (b coefficients) of each individual plant species linear regressions for subset 1 (n=269 species, p-value≤0.05). See Figure 3 for a comparison of density distribution functions between locations.

Location	No. species	Range b	Range R^2
Negative			
Lacandona, Mexico	64	-1.04 to -0.0003	0 to 0.99
Tuxtlas, Mexico	74	-0.71 to -0.005	0 to 0.5
Usina Serra Grande, Brazil	15	-0.44 to -0.006	0 to 0.67
Total species	**153**		
Positive			
Lacandona, Mexico	31	0.0004 to 0.34	0 to 0.6
Tuxtlas, Mexico	75	0.005 to 0.6	0 to 0.95
Usina Serra Grande, Brazil	6	0.1 to 0.4	0.01 to 0.25
Total species	**112**		
Zero			
Lacandona, Mexico	1	-	0.65
Tuxtlas, Mexico	3	-	0.45 to 0.53
Usina Serra Grande, Brazil	-	-	-
Total species	**4**		

Table 2. Significant slopes (b coefficients) of each individual plant species linear regressions for subset 2 (p-value≤0.05) including and excluding zero patches on each separate location. See Figure 6 for a comparison of density distribution functions between locations.

	Zero patches			No zero patches		
Location	No. species	Range b	Range R^2	No. species	Range b	Range R^2
		Negative			Negative	
Garuke, Ethiopia	26	-0.34 to -0.02	0 to 0.5	5	-7 to -0.27	0.01 to 0.21
Tigray, Ethiopia	22	-0.95 to -0.001	0 to 0.8	7	-0.75 to -0.1	0.01 to 0.24
Taita Hills, Kenya	67	-0.64 to -0.03	0.005 to 0.96	11	-0.74 to -0.02	0.1 to 0.55
		Positive			Positive	
Garuke, Ethiopia	2	0.1 to 0.12	0.05 to 0.1	-	-	-
Tigray, Ethiopia	18	0.02 to 0.96	0 to 0.63	2	0.1 to 0.4	0.01 to 0.26
Taita Hills, Kenya	15	0.01 to 0.41	0.001 to 0.7	1	0.12	0.2
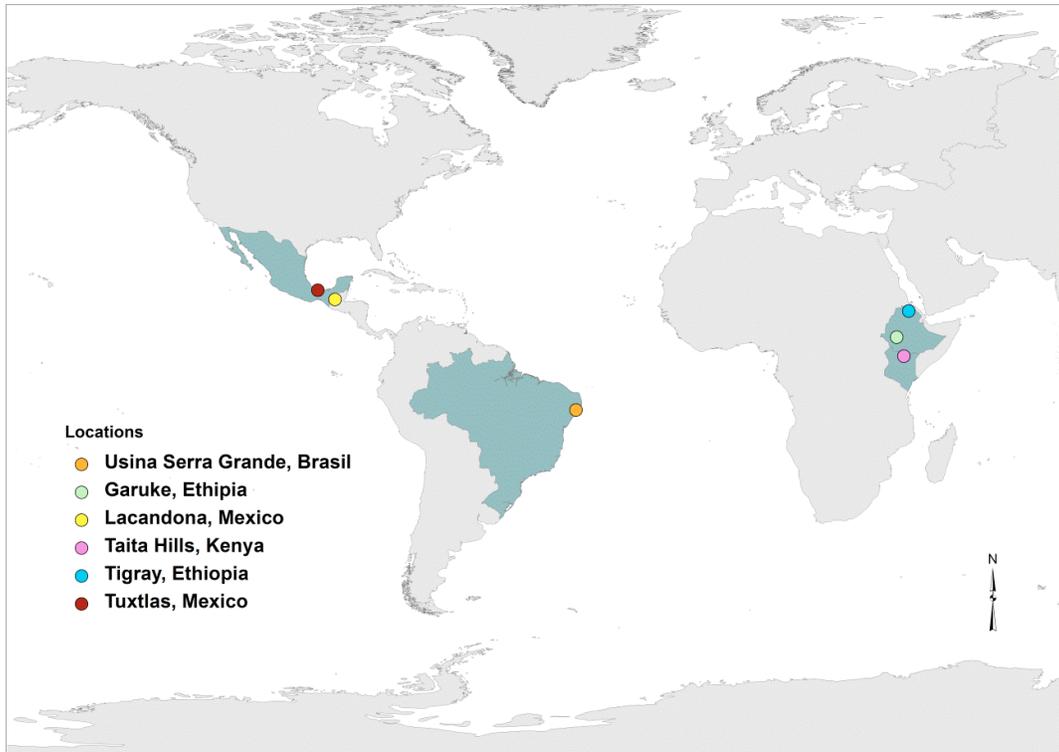
Figure 1. Location of the patch areas analysed. Projection: WGS 1984
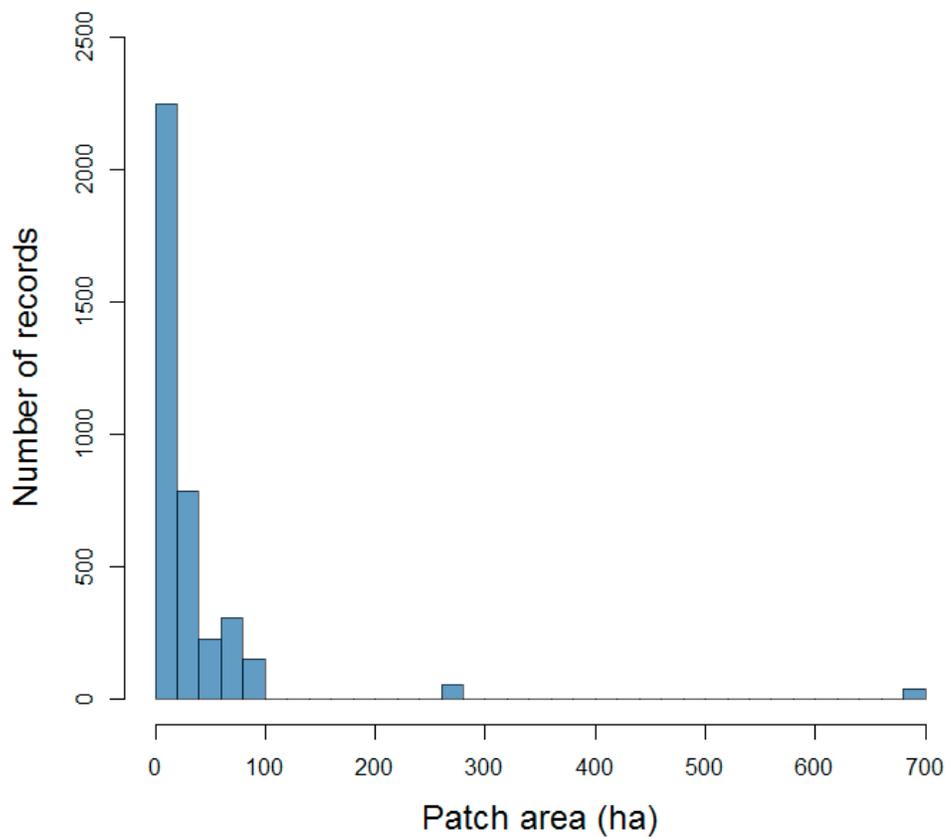
Figure 2. Distribution of patch areas for all data set. N=5,708 records. Patch areas are not log-transformed to show the actual distribution of the areas.
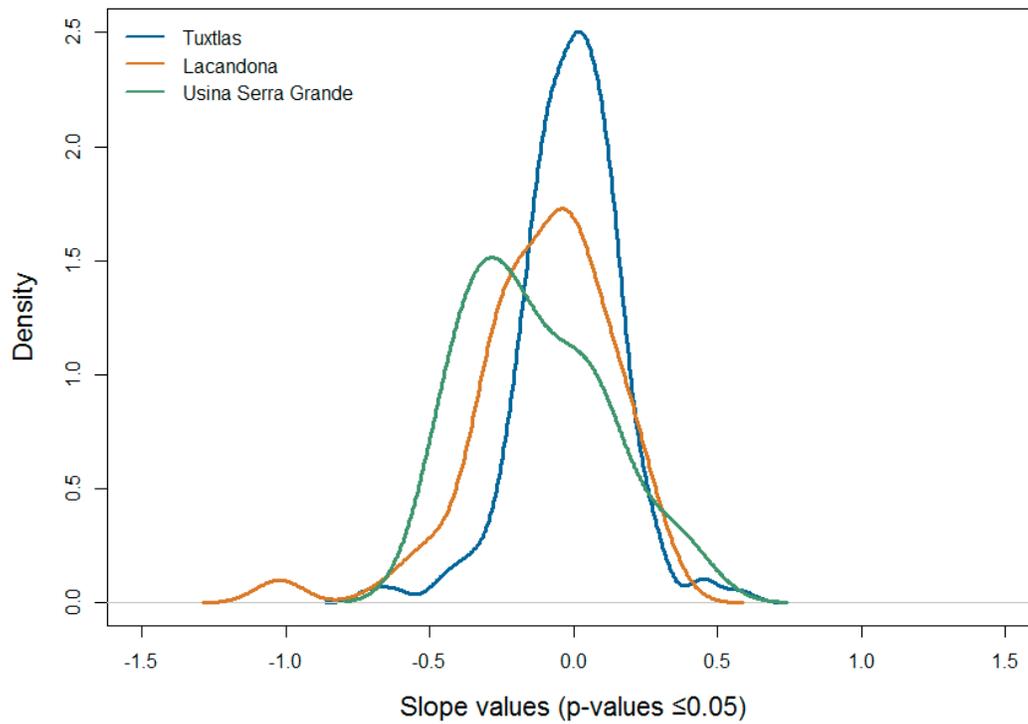
Figure 3. Distribution of the significant slope values (p-values ≤ 0.5) between locations for subset 1. The probability density function was calculated using Kernel density estimation as in R documentation (2015).
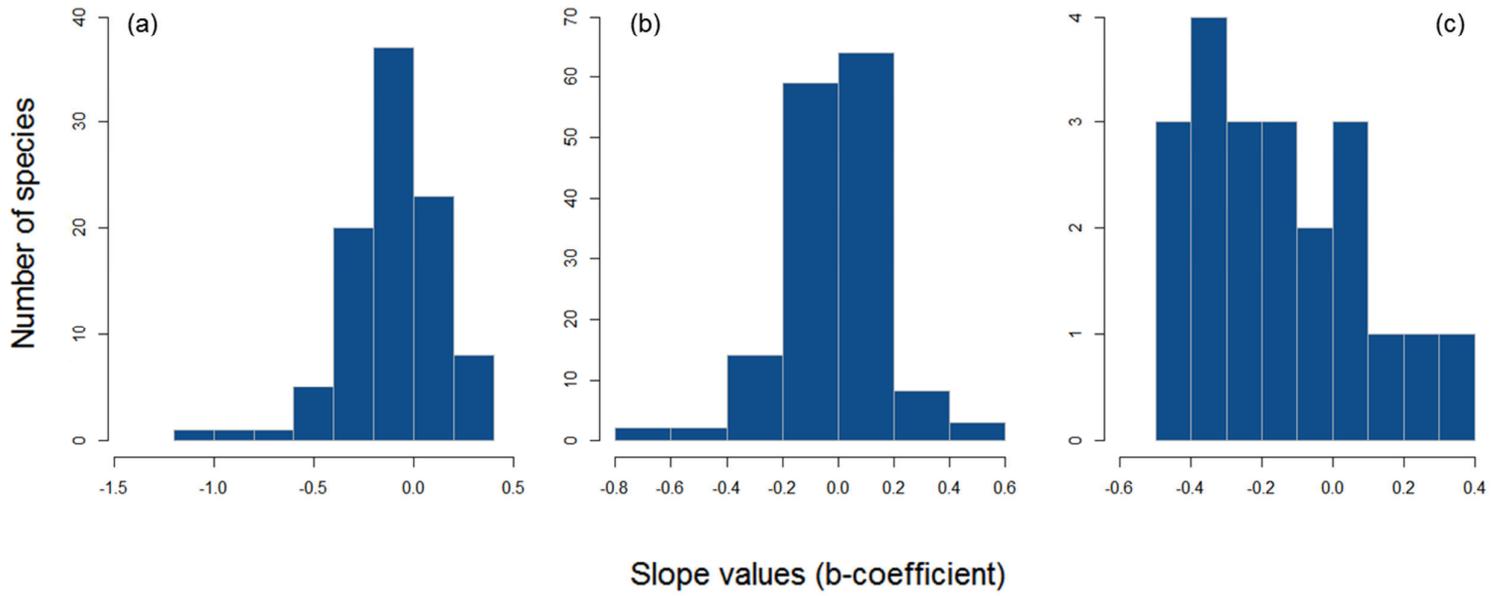
Figure 4. Distribution of slope values from species with significant density patch-area relationship (p-values ≤0.05) for subset 1, an separated by location, (a) Lacandona, Mexico, (b) Tuxtlas, Mexico and (c) Usina Serra Grande, Brasil.
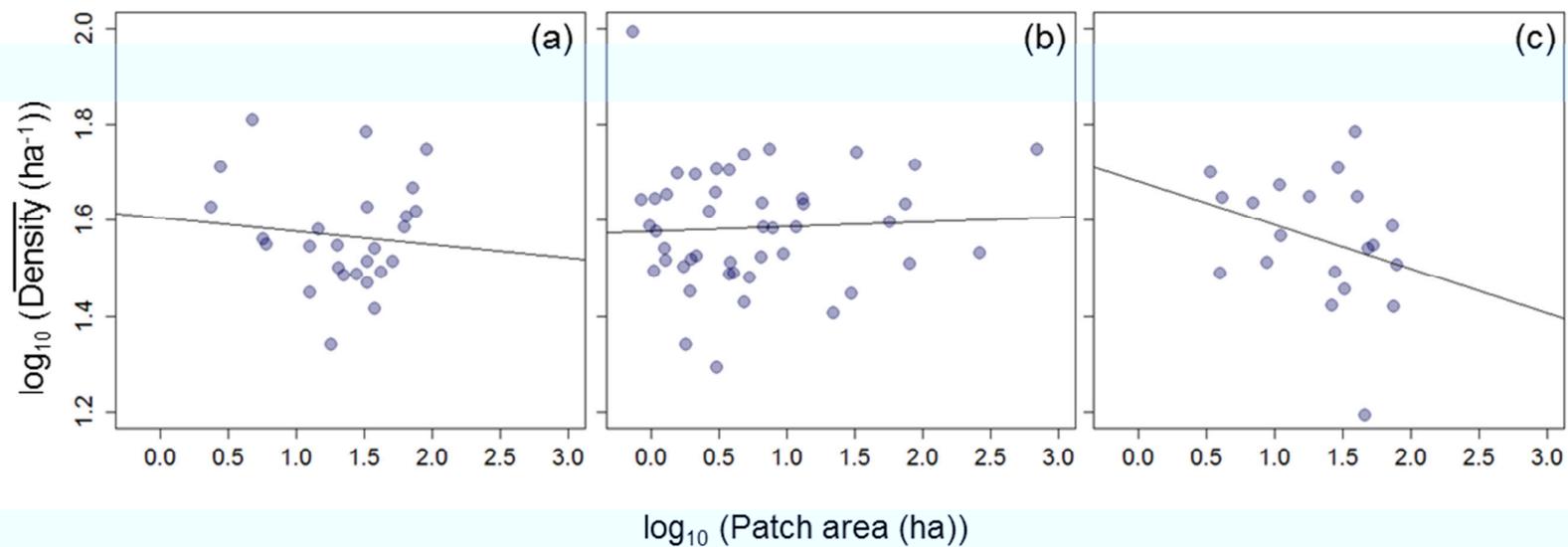
Figure 5. Relationship between the average densities per species and patch area, calculated per each individual location in subset 1. (a) Lacandona, b.Lacandona= -0.03, C.I.: 95%: - 0.133 to 0.08; (b) Tuxtlas, b.Tuxtlas = 0.009, C.I.: 95%: -0.045 to 0.065, and (c) Usina Serra Grande, Brasil, b.Usina = -0.1, C.I.: 95%: -0.23 to 0.05).
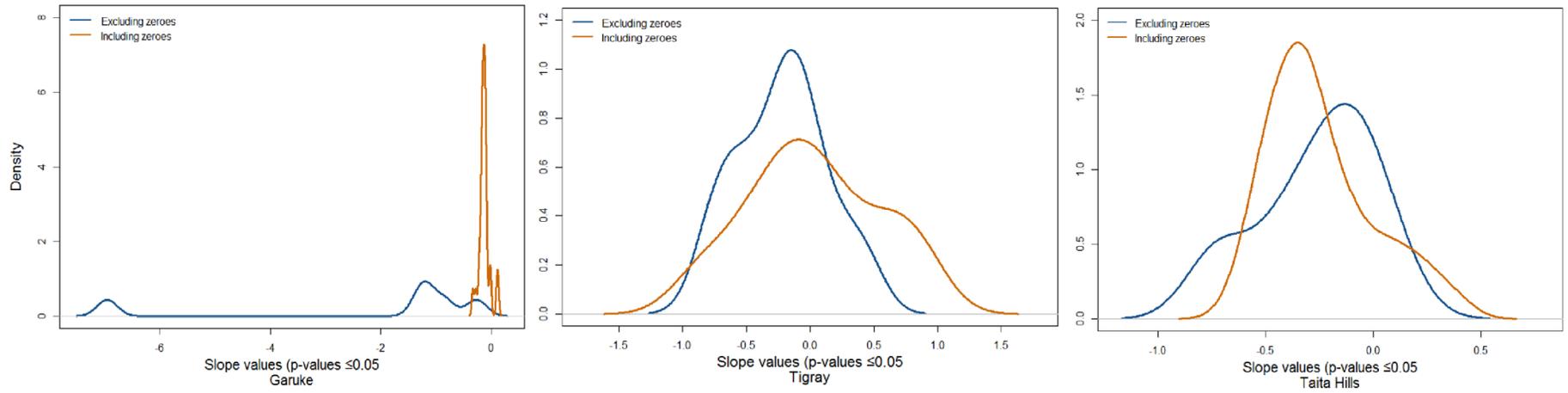
Figure 6. Distribution of the significant slope values (p-values ≤ 0.5) between locations for subset 2. The probability density function was calculated using Kernel density estimation as in R documentation (2015).

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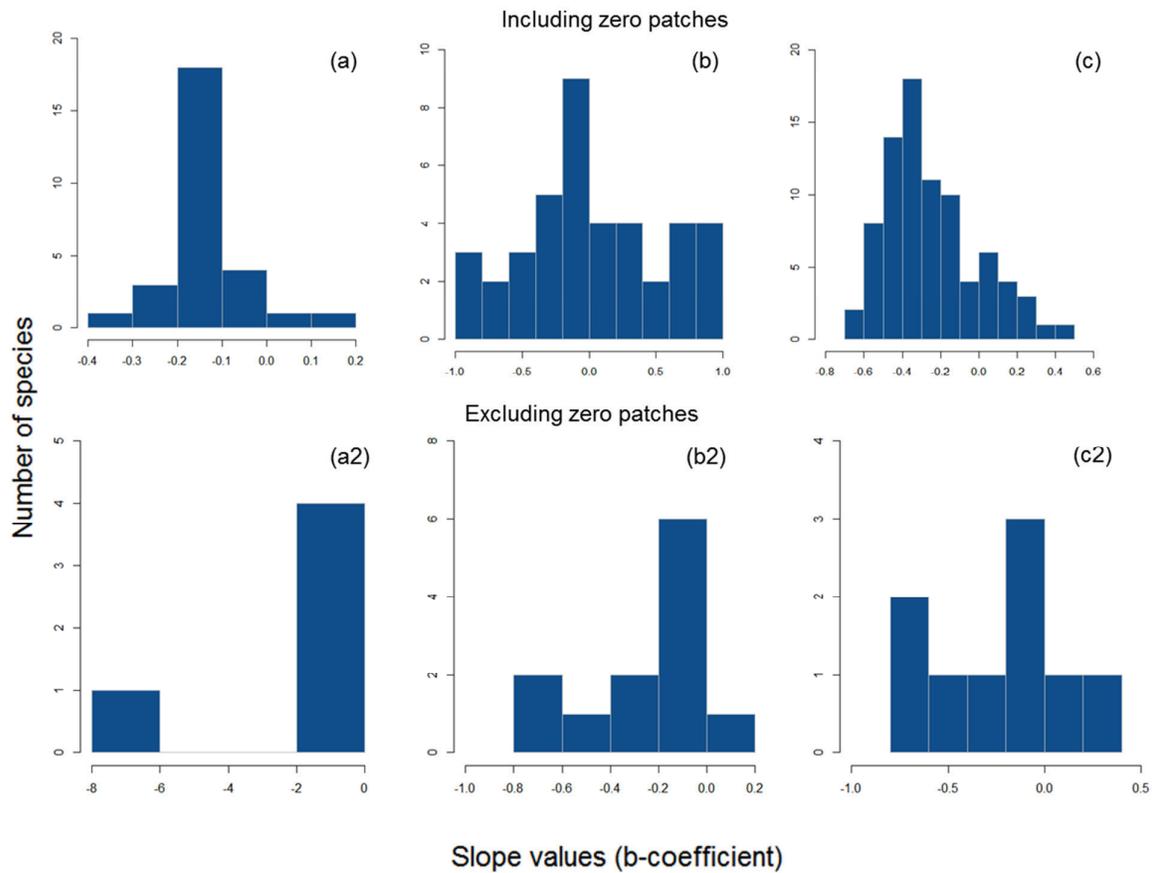
Figure 7. Distribution of slope values from species with significant density patch-area relationship (p-values ≤0.05) for subset 2, separated by location and by including or excluding zero patches, (a) and (a2) Garuke, Ethiopia, (b) and (b2) Tigray, Ethiopia, and (c) and (c2) Taita Hills, Kenya.

CHAPTER 4

The initial proposal for my thesis included additional inquiries to test for diverse abundance-based macroecological patterns for plant species beyond individuals-area relationships. Having completed the analyses for chapters 2 and 3, it became clear that there was too little data available to be sufficient for the attempted inquiries.

In the following chapters I am therefore exploring a collection of data sets to examine other macroecological patterns for plants at diverse spatial scales and their interactions with anthropogenic activities.

In the fourth chapter I examine how past human activities affect species richness in a long-term managed landscape: Cornwall, UK.

Maria Eugenia Correa-Cano, Emma Trevarthen, James P. Duffy, Jonathan Bennie, Richard Inger, Kevin J. Gaston. **Plant species richness and the historical landscape of Cornwall, UK.** *In prep.*

Authors' contributions:

Conceived and design: MEC-C, KJG

Data provision: ET

Data analysis: MEC-C, JPD

Draft chapter: MEC-C

PLANT SPECIES RICHNESS AND THE HISTORICAL LANDSCAPE OF CORNWALL, UK.

ABSTRACT

Past anthropogenic activities have proven to have a marked impact on current levels of plant species richness at local scales. Logically, such effects should extend to landscape scales. However, a paucity of appropriate historical data has constrained the opportunities to undertake such analyses. Here, we exploit an exceptional historical land use data set for Cornwall, UK, to evaluate the proportion of variation in current plant species richness explained by long-term anthropogenic activities in the county at two spatial scales, 10km x 10km and 2km x 2km. After controlling for spatial autocorrelation, we found a significant negative relationship at 10km x 10km between species richness and landscapes predominately shaped by human activities in the 17th and 19th centuries, namely ornamental activities, which together with upland woods explained a high proportion of the variation in current plant species richness (50%). We also found that upland woods and the total land area of a grid cell were significant terms explaining species richness at 2km x 2km, although the model at this resolution explained only 5% of the total variation. The number of different historical landscapes in the county did not have a significant effect on plant species richness at either spatial resolution. The retention of current broad patterns of species richness in current landscapes may require careful consideration of how those landscapes were historically shaped over long periods.

INTRODUCTION

It is undeniable that anthropogenic activities have an important negative impact on landscapes throughout the world. Globally, biodiversity loss is one of the most conspicuous consequences of some of the impacts from anthropogenic actions, such as effects from land use change, habitat reduction, climate change and atmospheric deposition (Sala et al. 2000, Foley et al. 2005, *WIREs Clim Change,* 2014). There is additional evidence showing that contemporary conditions are not sufficiently explaining variation in plant species richness. For example, Motzkin et al. (1996, 1999), Campton et al. (1998), Donohue et al. (2000) and Eberhardt et al. (2003), all showed that history of past-land use exerts persistent influence on modern vegetation on sand plain ecosystems in the north-eastern US. Assessments of forests in the north of America and Europe have demonstrated how past agricultural and livestock husbandry activities have driven the impoverishment of soils, causing changes to the ability of the land to support tree species belonging to old-remnant forests (Peterken & Game, 1984, Foster 1992, Harding et al. 1998, Honnay et al. 1999), decreasing rates of colonization from ancient forests to secondary forests (Keersmaeker et al. 2014) and changing understory species composition (Brudvig et al. 2014). Considerable attention has been paid to elucidating how past human activities change soil composition, affecting floristic composition (Peterken and Game 1984, Hermy 1994) and stand structure (Foster et al. 1998, Glatzel 1991, Compton & Boone 2000, Dambrine et al. 2007, Prévosto et al. 2004).

There have also been a number of studies showing the effects of characteristics of the landscapes nearby study areas (e.g. isolation, surrounding landscape) on current

species richness, suggesting the importance of broader scale influences (Hüttler & Schaaf 1995, Cousins & Eriksson 2001, Söderström et al. 2001; Krauss et al. 2004, Öster et al. 2007; Cousins & Aggemyr 2008, Aggemyr & Cousins 2012). Variables explaining plant species richness are scale dependant as the processes driving patterns at different scales can vary, such that meaningful comparisons of studies performed at different scales are not possible (Willis & Whittaker 2002, Ochoa-Ochoa et al. 2014). Particularly well known is the fact that species richness and inferences made from its measurement are scale dependent (Noss 1983, Wilson & Schmida 1984, Conroy & Noon 1996, Whittaker et al. 2001).

To date the majority of the studies of historical land-use effects on current species richness have been made at a local scale (e.g. Hill & Jones 1978, Gomez-Pompa et al. 1987, Koerner et al 1997, Eriksson 1998, Austrheim et al. 1999, Honnay et al. 1999, Bellemare et al. 2002, Parker et al. 2010, Ross 2011, Cook-Patton et al. 2014), and the consequences of past anthropogenic activities at a landscape level remain poorly explored. This is despite the fact that at a landscape level the spatial distribution of habitats is a key factor explaining species richness (Motzkin et al. 2002, Lindborg & Eriksson 2004), such that past landscape configuration is also likely to have an impact on present-day species richness (Aggemyr & Cousins 2002). Indeed, diverse gaps in studying the effects of historical land-use remain, because there are not enough case studies that help to determine any patterns of the effect of the history of land use on the number of species at the landscape level.

Determining the proportion of the variation in plant species richness that is explained by historical and recent anthropogenic activities at the landscape level is a

keystone in the study of the effects of past land use. Nevertheless, at the landscape level, well-documented information on past land-use or land-use configuration is constrained by the availability of records that accurately portray past human activities. Here, we determine the role of historical land use in shaping present-day plant species richness, using the landscape of Cornwall, UK, as a case study. This provides a particularly interesting basis for a study as the region has had a rich human history, which is still readily evident in the landscapes, and has not simply been erased by modern human activities.

The historic landscape of Cornwall was analysed and described in great detail by the Historic Environment Service of Cornwall Council and English Heritage in 1994, under the Historic Landscape Characterisation project. This study was the first to be undertaken in Britain (Cornwall Council 2011) in a program that included the concept of landscape 'character' as a way of describing change in the historic landscape (Fairclough et al. 1999), so that, this characterisation reflects the county as an historic landscape. One of the guiding principles of this characterisation is to study the present-day landscape as history not geography: the most important characteristic of landscape is its time-depth change and earlier landscapes exist in the present landscape. Landscapes are also considered as dynamic units, as management of change and not preservation (Clark et al. 2004). Under these principles, the long used landscape of Cornwall is remarkably complex, filled with structures, patterns, and communities (human and semi-natural), all overlaid by varied personal and communal perceptions, interpretations and meanings (Herring, 1994). The Historic Landscape Characterisation project does not define the former extent of ancient systems; rather it illustrates the

surviving character of land-uses in today's landscape. These land-uses originate from specific periods in time (prehistoric, medieval or more recent). The characterisation provides an interpretation of the whole landscape and the processes of human actions that have shaped landscapes through time, and allows all land-uses to be given archaeological significance in a landscape scale (Cornwall Council 2011). This historical landscape data for Cornwall is unique. Indeed, most available information regarding past anthropogenic activities on landscapes does not include the remaining character over time and/or the processes through time.

These historically overlapped and complex landscape units are named Historical Landscape Characters (HLC). In the present study, we considered these units (HLC) to answer the questions of: What is the proportion of the variation in plant species richness explained by the Historical Landscape Character in Cornwall? Are there significant differences in the number of species between areas of Historical Landscape Characters originating in different time-periods? Is the variation better explained by the diversity of landscape character rather than a single landscape character? How do these patterns change with spatial resolution?

METHODS

Study area

Cornwall forms the western most part of the South West peninsula of the United Kingdom, bordered to the north and west by the Celtic Sea, to the south by the English Channel, and to the east by the county of Devon, over the River Tamar (Figure 1). The

landscape of Cornwall, covering an area of 3,563 square kilometres, is predominantly rural in character, and supports a mixed farming regime. Agriculture takes up 80% of the land. There are areas of unenclosed moorland; the most extensive occurs in the Bodmin Moor uplands, but there are smaller areas on the Lizard Pensinsula and in West Penwith. There is only a limited amount of woodland, largely confined to the river valleys, but with some forestry plantations in the north and northeast of the county. The county has a population of 532,300 people (https://www.cornwall.gov.uk/council-and-democracy/data-and-research/data-by-topic/population/) and contains only one city, Truro.

Plant species

Plant species data occurrences for Cornwall were derived from ERICA (Environmental Recording in Cornwall Automated), a large data base containing records from a diverse array of taxa for Cornwall (ERCCIS, 2013). We considered all vascular and non-vascular records from 1970 to 2004, since the collection effort is considered to be reasonably even and the methodology reasonably standardized for this period but not before (Rich & Woodruff 1996). We evaluated records at 10km x 10km (hectads) and 2km x 2km (tetrads) resolutions. The base methodology of plant species data collection in Cornwall is the same as the one established by the Atlas of the British Flora; plant species are recorded independently from hectads than from tetrads (Preston et al. 2002). While records at 10km x 10km has been the base methodology to carry out collection of plant species for the Atlas of the British Flora, records at 2km x 2km

resolution were collected independently from local floras and checklists, information that

has been integrated into atlases independently of the recording in hectads. Therefore,

integrating both resolutions into the analysis would seem sensible to give insights into

the effect of scale. We evaluated a total of 981 plant species, considering aggregates,

species *sensu lato* and subspecies as per Preston et al. (2002).

Historic Landscape Character of Cornwall

Information regarding the history of the landscape in Cornwall was obtained from the

Historic Environment Service of Cornwall Council (Cornwall Council 2011). Spatial

layers of historical information for Cornwall are available as Historic Landscape

Character types (HLC-types) and zones (HLC-zones, Figure 1). The HLC-types include

20 detailed historical layers (Figures 2 & 3), and the HLC-zones include 15 historical

layers which enclosed nine of the HLC-types in broader categories (Figure 1 & 2). A

brief explanation of the characteristics of each type is given in Table A3.1, Appendix 3

(see Herring 1994, Fairclough et al. 1999, Cornwall Council 2011 for a detailed

explanation of each HLC type and the methodology).

Data processing

We used ArcMap (ESRI 2010) for data processing unless otherwise specified. We

analysed the historical landscape information by 1) considering the HLC-types clustered

in four time categories and 2) considering the 15 HLC-zones (which are originally

merged from the Cornwall Council project; 2011). For the analysis with the HLC-types,

we merged the number of explanatory variables (20 originally) with the purpose of

decreasing the number of parameter estimates given its large number, which is 54% of the number of grid cells at hectads (37), so that including all the variables might lead to a lack of degrees of freedom and to an over-fitted model. Therefore, we grouped 18 of the 20 HLC-types into four time categories: i) Ancient (from Iron Age to 17th Century), ii) 17th to 19th centuries, iii) 20th Century, and iv) Industrial (Figures 3 & 4). These categories reflect four main time periods in the history of the Cornish landscape and were established based on the documentation given by Cornwall Council (2011). The first category (Ancient) encompasses the most ancient collection of anthropogenic land use recorded in the county. The rough ground industrial type contained in the Ancient category is referring mainly to areas where relict industrial landscape has been overwhelmed by woodland or has become upland rough ground. Inasmuch as the oldest history of the rough ground industrial type is related to activities dated since the Iron Age, we decided to include the remnant areas in the ancient merged layer. Character types in the second category (17th to 19th centuries) include farmland during the Post Medieval period, the records of settlements before the 20th Century and ornamental activities that refer mainly to plantations in parks and private gardens. For the third category (20th Century), we included ancient woodland, which, despite the name, corresponds to woodlands mainly created by humans during this period or to the enhancement of old forested areas through reforestation. See Figure 3 for the other types belonging to this category. Industrial activities, which are mainly defined as extractive industry in Cornwall (mining and quarrying), were merged into a single fourth category.

The remaining two HLC types, communications and natural water, were not merged in any category. Continuous changes to communications make it very difficult to merge them into a precise period and sources of natural water have existed before humans arrived in the territory and have played a very important role in the development of different cultures during all times. We use character type, landscape type and land-use interchangeably.

Although we are statistically avoiding a lack of degrees of freedom and thus over-fitting our model, the time-merged HLC-types layers might be inaccurate given that the landscape has been continuously modified and that the finding of one kind of land-use does not imply the exclusion of others. To avoid the probable inaccuracy of time-merged HLC-type layers, we considered also the HLC-zones in a separate analysis. These zones are historical layers of information previously grouped by the HLC project (Cornwall Council 2011). These include: military, ancient woodland, anciently enclosed land, recently enclosed land, coastal rough ground, communications, dunes, ornamental, predominantly industrial, recreation, water reservoirs, upland rough ground, upland woods, urban and residential developments, and water natural (Figures 1& 2).

Plant species records and HLC layers (types and zones) were re-projected onto the British National Grid coordinate system to perform all of the analyses. Plant data records were subdivided by considering 10km x 10km and 2km x 2km resolutions. Two grids covering Cornwall were created spatially to locate plant data, each corresponding to one resolution. Each data set was in turn processed to translocate the information storage at the left corner of a grid cell to its geographic centre. For each grid cell at both resolutions we calculated the area covered by each HLC time category and the species

richness. Given the disproportionately small amount of land in coastal grid cells, and the likelihood of obtaining an artefactual pattern in the results as a consequence of the increase of area of land grid cells, we only kept grid cells with ≥50% of land. Thus, species richness was extracted on a total of 37 out of 65 grid cells for hectads and 907 out of 1,034 grid cells for the tetrad resolution (Figure 5). Data extraction was performed in R (R core team, 2015), using the package 'foreign' (Bivand et al. 2015).

Statistical Analysis

The following processes were performed at tetrads and hectads scales. To account for the variation in species richness explained by the historical landscapes of Cornwall, two independent multiple linear regressions between species richness and 1) the total of merged HLC-types area (fixed factor, 6 levels; ancient, 17th-19th centuries, 20th Century, industrial, communications, water natural), and 2) the total of HLC-zones area (fixed factor, 15 levels; military, ancient woodland, anciently enclosed land, recently enclosed land, coastal rough ground, communications, dunes, ornamental, predominantly industrial, recreation, water reservoirs, upland rough ground, upland woods, urban and residential developments, water natural, communications, water natural) were created. To further account for the possible effect of the disproportionate increase of area of inland tetrads and hectads we added the total area of land occupied per each grid cell (in their corresponding scale) as an additional variable in both multiple linear regressions. All variables (explanatory and response) were logarithmic transformed to better approximate normality (Zuur et al. 2007). To take account of zero values under

log transformation, we added 1 to the explanatory variables. Additionally, sets of independent OLS regressions were performed between species richness and the area covered by each merged HLC type (6 models) and between species richness and the area represented by each of the HLC-zones (15 models). Also, two general OLS models of the relationship between species richness and the total summed area of merged HLC types and between the total summed area of HLC-zones were performed.

Spatial autocorrelation (SA) is present in most spatial data in ecology (Lennon 2000). If it is ignored, the analysis can produce misleading results given that it can invalidate the assumptions of independent errors in a linear regression model and might affect parameter estimates (Lennon 2000, Legendre et al. 2002, Dormann et al. 2007). SA may occur in the response variable of our data (species richness) or at a landscape level (merged HLC types or HLC-zones). Records from contiguous cells might be spatially autocorrelated, particularly in areas where an overlap of the distribution ranges of the species or of the merged HLC types or HLC-zones exists. In addition, underlying dispersion processes in the Cornish vegetation, which are not considered in this analysis, might play an important role. We used Moran's I statistic to determine the existence of spatial autocorrelation within the residuals of the independent errors models, and applied this to a spatial model, considering species richness as the response variable and the area of each merged HLC type or HLC-zone. Where SA was found, we used the Lagrange Multiplier diagnostic (Anselin, 1988) to determine the appropriate model. We also tested for SA in the explanatory variables (at landscape level) by applying a SAR-mixed model (Kissling & Carl 2007). We applied a Breusch-Pagan test for heteroscedasticity (Breusch & Pagan 1979) in the final models.

Calculating the proportion of the variation explained by spatial models is problematic, given that errors by definition are correlated. Nevertheless, here we applied the Nagelkerke function implemented in the 'spded' package to calculate a pseudo-R-squared as an indication of the proportion of the variation explained by the HLC-types. We used the 'spdep', 'Spatial', 'maptools', 'rgdal' and 'lmtest' packages in R (2015) when testing for SA.

RESULTS

We analysed a total of 981 plant species. The average number of plants in hectads was 380.2, ranged from 286 to 611, and from 1 to 97 in tetrads, with an average of 45.75 species (Figure 5a). A broadly left-skewed distribution of species richness for hectads was observed (Figure 5b) which differed from the nearly normally distributed richness at tetrad level (Figure 5c).

Under the multiple linear regression models, only the total area of a grid cell at tetrad scale for both sets of explanatory variables (merged HLC types and HLC-zones) was slightly significant (b=0.4, 95% CI: 0.06 to 0.7 and b=0.4, 95% CI: 0.05 to 0.74). None of the merged HLC types or the HLC-zones categories was significant in explaining current species richness at either resolution.

The independent OLS regressions considering the six merged HLC types and the total area of each cell grid at hectad resolution showed that the categories merged in the 17th to 19th centuries were negatively related to current species richness (b=-0.1,

95% CI: -0.17 to -0.02, Table 1). None of the merged HLC types at tetrad resolution were significant for current species richness (Table 1).

The independent OLS regressions considering the 15 HLC-zones and the total area of each grid cell at hectad resolution showed that upland rough ground zone was significantly negatively related to species richness (b=-0.043, 95%CI: -0.08 to -0.001, see Table 2 for non-significant terms). The category dunes was excluded from the analysis at this resolution given that only 2 grid cells contained this zone after considering the threshold of 50% of land. At tetrad scale, none of the HLC-zones explained current species richness (Table 2).

The linear regression between species richness and the total area covered by the merged HLC types was not significant at either resolution (at hectads: $\log_{10}$(No.spp) = 2.75 + -0.04$\log_{10}$HLC(km^2), R^2= -0.02, 95% C.I. -0.3 to 0.2, F-statistic$_{1,35}$=0.13 at tetrads: $\log_{10}$ (No.spp) = 1.5 + 0.21$\log_{10}$HLC(km^2), R^2=0.001, 95% C.I.: -0.06 to 0.47, F-statistic$_{1,905}$=2.362). Also, no significant relationship was obtained between these variables when considering HLC-zones at either resolution (at hectads: $\log_{10}$ (No.spp) = 2.75 − 0.04$\log_{10}$HLC(km^2), 95%CI: -0.3 to 0.2; at tetrads: $\log_{10}$(No.spp) =1.5 + 0.2 $\log_{10}$HLC(km^2), 95%CI: -0.06 to 0.5).

The number of merged HLC types ranged from 4 to 6 in hectads and from 1 to 6 in tetrads (Figure 6). The number of HLC-zones in hectads ranged from 8 to 15 in hectads and from 1 to 11 in tetrads (Figure 6). The number of land uses in Cornwall did not explain species richness significantly at either resolution, or under any model (HLC-merged types at hectads: $\log_{10}$ (No.spp) = 2.6 + 0.01 land use richness, 95%CI: -0.025

to 0.045; at tetrads $\log_{10}$ (No.spp) = 1.67− 0.01land use richness, 95%CI: -0.03 to 0.006; HLC-zones at hectads: $\log_{10}$ (No.spp) =2.65 + 0.001 land-use richness, 95%CI: -0.014 to 0.016; at tetrads: $\log_{10}$ (No.spp) = 1.63 + 0.0002 land use richness, 95%CI: -0.008 to 0.009).

Significant spatial autocorrelation in the residuals of the linear models was obtained for both resolutions (merged HLC types model for hectads: Moran's I=5.8, p-value=0.02; tetrads: Moran's I=5.8, p-value<0.001; HLC-zones model for hectads: Moran's I=2.1, p-value=0.02, tetrads: Moran's I= 4.8, p-value<0.001). At a hectad resolution no SA remained after running the SAR-mix model for the merged HLC types (rho=0.3, p-value=0.3). No remaining heteroscedasticity in the residuals was left (studentized Breusch-Pagan test BP=5.6, p-value=0.6). Under this spatial model, only the 17th to 19th centuries merged HLC- type proved to be significant (and negatively related) in explaining species richness (b=-0.14, SE=0.1, p-value=0.04). Nagelkerke pseudo R-squared for this model explained 25% of the variation. At tetrad resolution, the SAR-mix model showed no remaining SA (rho=0.1, p-value=0.1), although no HLC variables significantly explained plant species richness (non-significant variables are not reported). This model also explained a low proportion of the variation (Nagelkerke pseudo R-squared=0.01).

Regarding HLC-zones, at hectad and tetrad resolutions no SA remained after running the SAR-mix model (rho=0.4, p-value=0.2 and rho=0.002, p-value=0.9, respectively) and no heteroscedasticity remained in the residuals (BP=16.4, p-value=0.43 and BP=12.96, p-value=0.7). At hectad resolution, two variables proved to be significant in explaining species richness, ornamental and upland woods

($\log_{10}$Ornamental: b=-0.01, p-value=0.03; $\log_{10}$Upland Woods: b=0.2, p-value=0.01). The total variation explained by this model is 50% as given by Nagelkerke pseudo-R-squared. At tetrad resolution Upland Woods and grid cell area significantly contributed to explaining current plant species richness (lag.$\log_{10}$Upland Woods: b=0.02, p-value=0.044; lag.$\log_{10}$Grid Area: b=1.1, p-value=0.02). However, total variation explained by this model was very poor (Nagelkerke pseudo-R-squared=0.05).

DISCUSSION

In this study, we assessed the proportion of the variation in current plant species richness that is explained by historic human activities in Cornwall at two different spatial resolutions and considering two categorisations of land uses. Considering the merged HLC types at hectad resolution and after controlling for spatial autocorrelation, the 17th to 19th centuries category significantly explained a decrease in number of plant species. At the same scale but considering HLC-zones, ornamental activities (grouped under the 17th to 19th centuries category) also significantly explained a decrease of species richness. The ornamental zones in Cornwall are landscapes that have been deliberately and carefully manipulated. These include parklands, pleasure gardens surrounding large country houses, and ornamental plantations. These deliberate plantations include the constant removal of native and archaeophyte species (a plant species which is non-native to a geographical region, but which was introduced in "ancient" times, rather than being a modern introduction; Preston et al. 2002) through different land management activities. For instance, parklands are characterised by including a mix of grazed or mown lawns and scattered trees, and pleasure gardens are located usually immediately

around the house, both activities include a constant removal of non-desired species, and usually plantations of exotic species. These actions still continue in some ornamental areas in Cornwall until now. Very few ornamental plantations remain that are used as shelter belts, frames for views, cover for game, and as sources of timber; which might promote the occurrence of native species. There is no further evidence from the analysis that indicates that other types merged in the 17th to 19th centuries category are significant determinants of species richness. Under the HLC-zones analysis, upland woods at hectad and tetrad scales significantly explained variation in current plant species richness. These woods are located on the zones of the upland rough ground which are no long grazed, so that secondary woodland has been able to develop. These abandoned areas can also be overgrown with gorse or scrub, and it is not clear from the maps or from the HLC project itself that there is a distinction between these types of vegetation. However, the abandonment of traditional activities on land may lead to a return of the surrounding vegetation promoting the occurrence of a larger number of species in upland rough ground zones.

Total grid area at tetrad scale under the HLC-zones model was significant in explaining current plant species richness. This suggests that at tetrad resolution total area is more important than the land-use types (apart from the significant zones variables explained above) when considering current plant species richness.

Contrary to other studies carried out at landscape scale, there is no evidence that past landscape configuration also has an impact on present-day species richness (Aggemyr & Cousins 2002). The number of merged HLC types and HLC-zones in Cornwall did not explain variation in current species richness.

Differences between scales in these analyses are not clear. The scale-dependency of ecological patterns has been highlighted by several studies (e.g. Auerbach & Schmida 1987, Wiens 1989, Levin 1992, Crawley & Harral 2000). For example, the relationships between climate and vegetation that are evident at broad scales may disappear at finer ones, being overridden by the effects of competition and other biological processes (Greig-Smith 1979, Woodward 1987). Also, studies carried out at 1km x 1km and/or 5km x 5km quadrats in northern Finland showed that plant species richness was better explained by absolute latitude, length of watercourses, abundance of steep cliffs and gorges, and type of soil (Heikkinen 1996, Heikkinen & Birks 1996, Heikkinen & Neuvonen 1997, Heikkinen et al. 1998, Bruun et al. 2003). In contrast, studies carried out at larger scales (10km x 10km or larger) have shown that climatic and environmental variables play an important role in explaining numbers of plant species (Currie & Paquin 1989, Grytness et al. 1999, Nogués-Bravo & Araujo 2006). Our results indicate that some past human activities can also be important in explaining species richness at large scale (hectads): ornamental activities and upland woods are important for HLC-zones. At tetrad scales, past human activities are not important in explaining species richness, as only the total area of a tetrad and the lag-term for upland woods explained species richness (for the same grouped data). It is Important to recall that the relative importance of the lag-term upland woods at tetrad scale may be an indication of the spatial autocorrelation of this HLC-zone with others. These areas are far from being homogenous and their historical management mirrors their heterogeneity. In addition to the regrowth into secondary forest after abandonment, upland woods have also been identified as plantations in what was previously upland

rough ground, which in turn depended on the use by occupants of other neighbouring HLC-zones for the last 3000 years. Particularly, farmers living in the ancient enclosed land used upland rough ground for their summer grazing grounds, and it was also a major source of fuel and stone. More recently, modern enclosed land zones have contributed to diminish the impact of past activities.

Although the plant species distribution data set used here is very detailed compared with most other parts of the world, many of the records were at the scale of grid cells of 10km x 10km and 2km x 2km, so we could not accurately determine which species occurred within which HLC types within a grid cell. This limitation prevented us from exploring which species characterised each HLC type or zone, and thus using this approach to understand the determinants of species richness in Cornwall. Nevertheless, within the constraints of our data, relatively recent historical activities showed a remarkable negative effect on plant species richness in Cornwall at 10 km x 10 km resolution, and there was a positive significant effect of upland woods on species richness at tetrad scale. This outcome should encourage future studies aimed at disentangling patterns of plant species diversity and distribution, function and/or sensitivity to change in land use in the county. As the effect of historical activities is scale dependant, it is highly recommended to consider the effective grain when detecting variability at landscape scale.

TABLES

Table 1. Coefficients from independent linear regressions between species richness and each HLC-merged type. The total grid area was also added as an explanatory variable. All variables were logarithmic transformed (base 10).

HLC-merged types	b	F-statistic $_{1,35}$	p-value	R^2	95% CI	Resolution
Ancient	0.04	0.287	0.6	-0.02	-0.1 to 0.18	
17th-19th Centuries	-0.1	6.845	0.01	0.14	-0.17 to -0.02	
20th Century	0.1	0.83	0.367	-0.004	-0.1 to 0.2	**Hectads**
Industrial	-0.001	0.03	0.86	-0.03	-0.01 to 0.01	
Communicatios	-0.002	0.14	0.71	-0.02	-0.01 to 0.01	
Water Natural	0.004	0.81	0.375	-0.005	-0.004 to 0.01	
F-statistic$_{1, 905}$						
Ancient	-0.005	0.05	0.824	-0.001	-0.06 to 0.044	
17th-19th Centuries	-0.002	0.18	0.67	-0.001	-0.01 to 0.006	
20th Century	0.003	0.05	0.82	-0.001	-0.02 to 0.02	**Tetrads**
Industrial	-0.003	0.8	0.36	0	-0.01 to 0.004	
Communicatios	-0.004	1.7	0.2	0.001	-0.01 to 0.002	
Water Natural	0.003	0.61	0.43	0	-0.004 to 0.01	

Table 2. Coefficients from independent linear regressions between species richness and each HLC zone (15 variables). The total grid area was also added as an explanatory variable. All variables were logarithmic transformed (base 10).

HLC-zones	b	F-statistic $_{1,35}$	p-value	R^2	95% CI	Resolution
Ancient woodland	0.02	4.1	0.05	0.07	-0.000 to 0.03	
Anciently enclosed land	0.1	2.33	0.14	0.04	-0.03 to 0.21	
Coastal rough ground	0.005	2.08	0.16	0.03	-0.002 to 0.012	
Communications	-0.002	0.14	0.7	-0.02	-0.014 to 0.01	
Military	-0.007	2.73	0.11	0.04	-0.01 to 0.002	
Ornamental	0	0.02	0.9	-0.03	-0.01 to 0.01	
Predominantly industrial	0	0.03	0.8	-0.02	-0.011 to 0.009	
Recently enclosed land	-0.11	3.72	0.06	0.07	-0.22 to 0.005	**Hectads**
Recreation	0.001	0.04	0.84	-0.03	-0.01 to 0.01	
Upland rough ground	-0.043	4.36	0.04	0.1	-0.08 to -0.001	
Upland woods	0.1	2.44	0.13	0.04	-0.02 to 0.2	
Urban and residential developments	0.01	0.5	0.5	-0.014	-003 to 0.055	
Water natural	0.003	0.8	0.37	-0.005	-0.00 to 0.01	
Water reservoirs	-0.005	1.32	0.26	0.01	-0.01 to 0.004	
F-statistic $_{1,905}$						
Ancient woodland	0.002	0.54	0.46	0	-0.003 to 0.008	
Anciently enclosed land	0.002	0.06	0.8	-0.001	-0.01 to 0.02	
Coastal rough ground	-0.0000136	0.00001365	0.9	-0.001	-0.007 to 0.007	
Communications	-0.004	1.694	0.193	0.001	-0.011 to0.002	
Dunes	0.003	0.05	0.8	-0.001	-0.02 to 0.03	
Military	0.01	2.8	0.09	0.002	-0.002 to 0.024	
Ornamental	0.002	0.3	0.6	0	-0.005 to 0.01	
Predominantly industrial	-0.003	0.5832	0.445	-0.005	-0.01 to 0.004	**Tetrads**
Recently enclosed land	-0.01	1.038	0.31	0	-0.023 to 0.01	
Recreation	0.002	0.4	0.55	-0.001	-0.005 to 0.01	
Upland rough ground	-0.003	1.53	0.216	0.001	-0.01 to 0.002	
Upland woods	0.007	3.54	0.06	0.003	-0.0003 to 0.014	
Urban and residential developments	-0.002	0.9	0.324	0	-0.01 to 0.003	
Water natural	0.002	0.61	0.435	0	-0.004 to 0.01	
Water reservoirs	0.003	0.3	0.58	-0.001	-0.007 to 0.014	

FIGURES
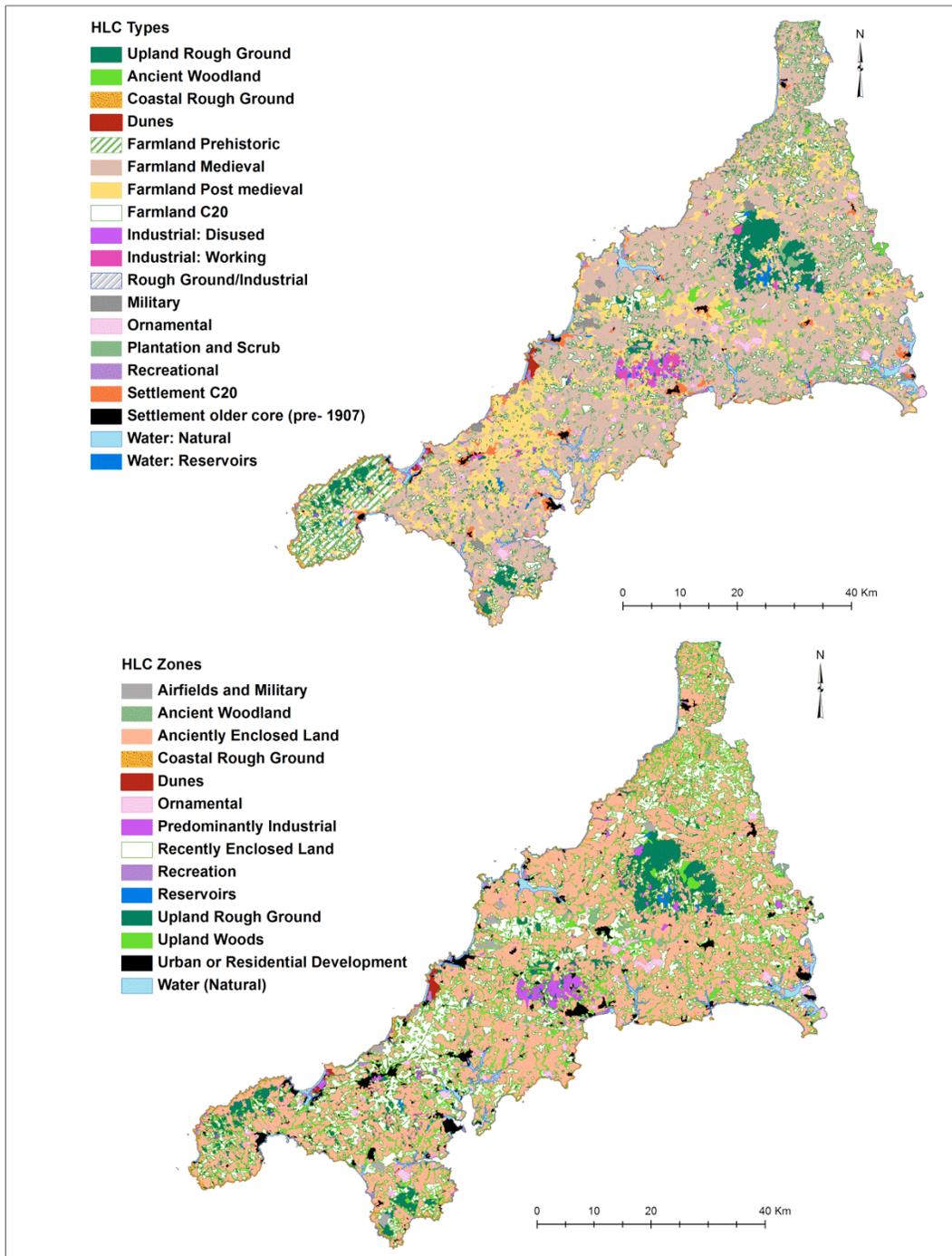
Figure 1. Map of the distribution of 19 of the 20 historic landscape character types of Cornwall and of the historic landscape character zones. Communications is not depicted on this figure.

HLC-types	HLC-zones	
Upland Rough Ground	Upland Rough Ground	
Coastal rough Ground	Coastal rough Ground	
Dunes	Dunes	
Ornamental	Ornamental	
Ancient woodland	Ancient woodland	
Plantations and Scrub	Upland woods	**Non-merged**
Military	Military	
Recreational	Recreational	
Water Reservoirs	Water Reservoirs	
Communications	Communications	
Water Natural	Water Natural	
Farmland Pre-historic	Anciently Enclosed Land	
Farmland Medieval		
Farmland Post Medieval	Recently Enclosed Land	
Farmland C.20		
Settlement old-core (Pre-20th Century)	Urban or residential development	
Settlement 20th Century		
Industrial working	Predominantly Industrial	
Industrial no-active		
Rough Ground Industrial		

Figure 2. Historic landscape character of Cornwall. Types and zones as delimited by the original project (Cornwall Council 2011).
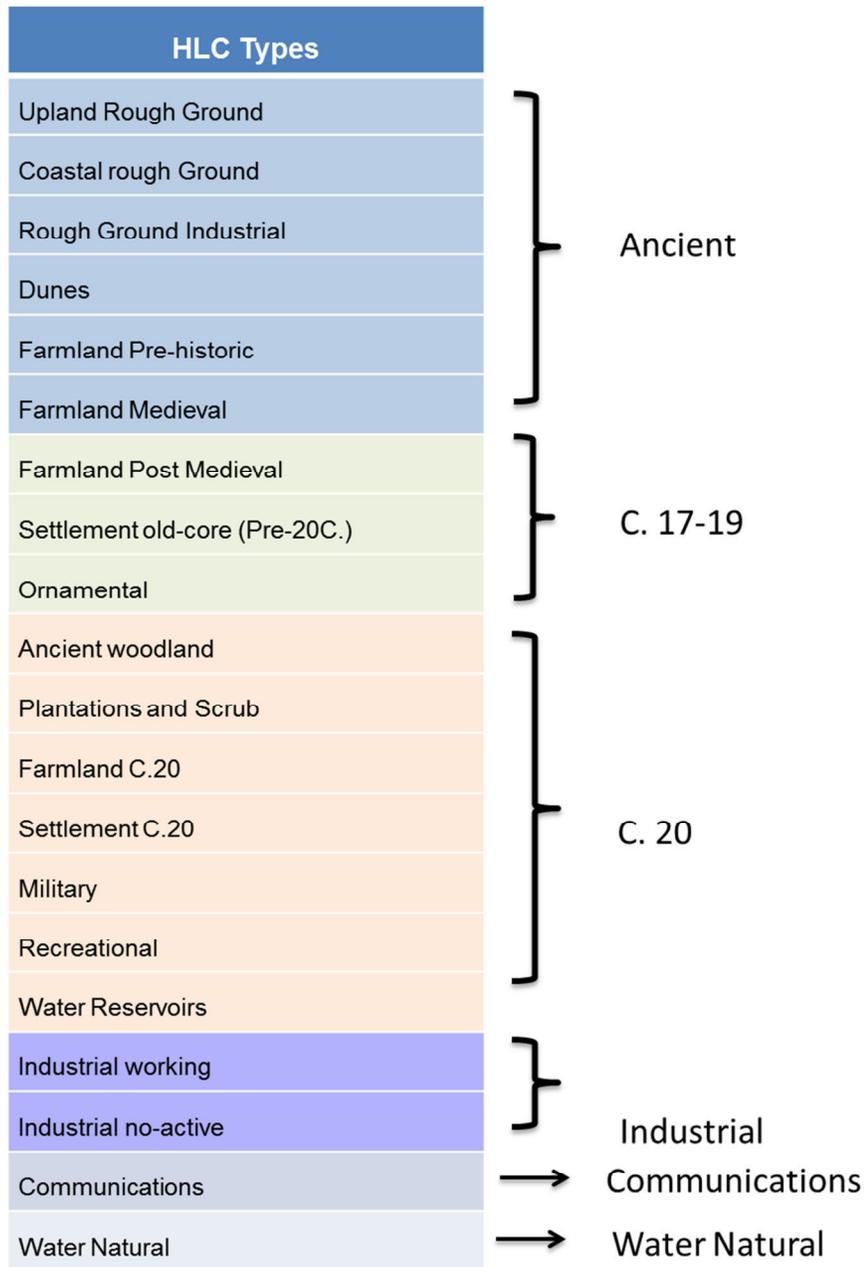
Figure 3. Historic landscape character types of Cornwall. Raw layers of information (left side) and the merged layers included on the analysis (right side).
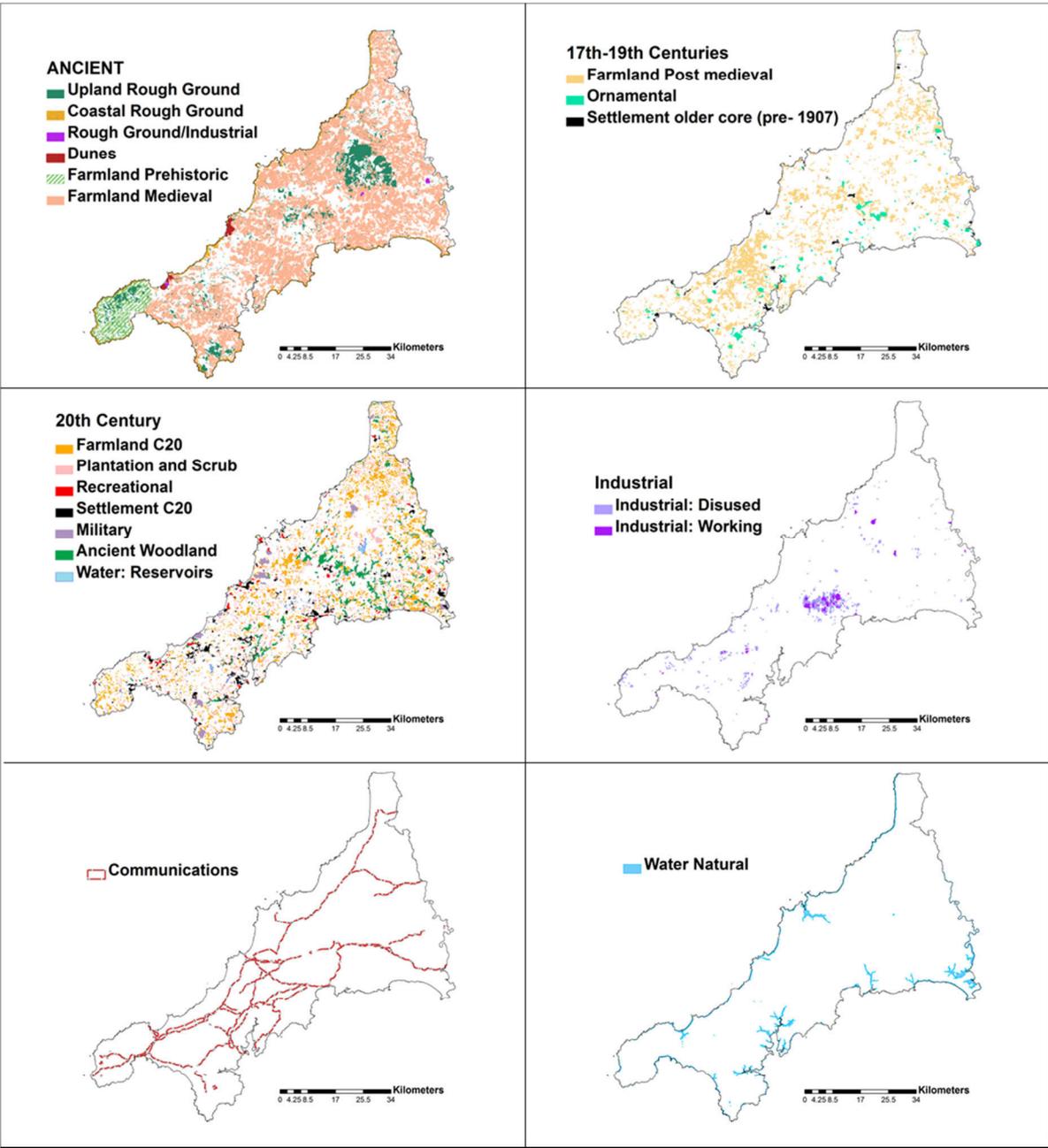
Figure 4. Maps of the merged historical landscape character types of Cornwall.
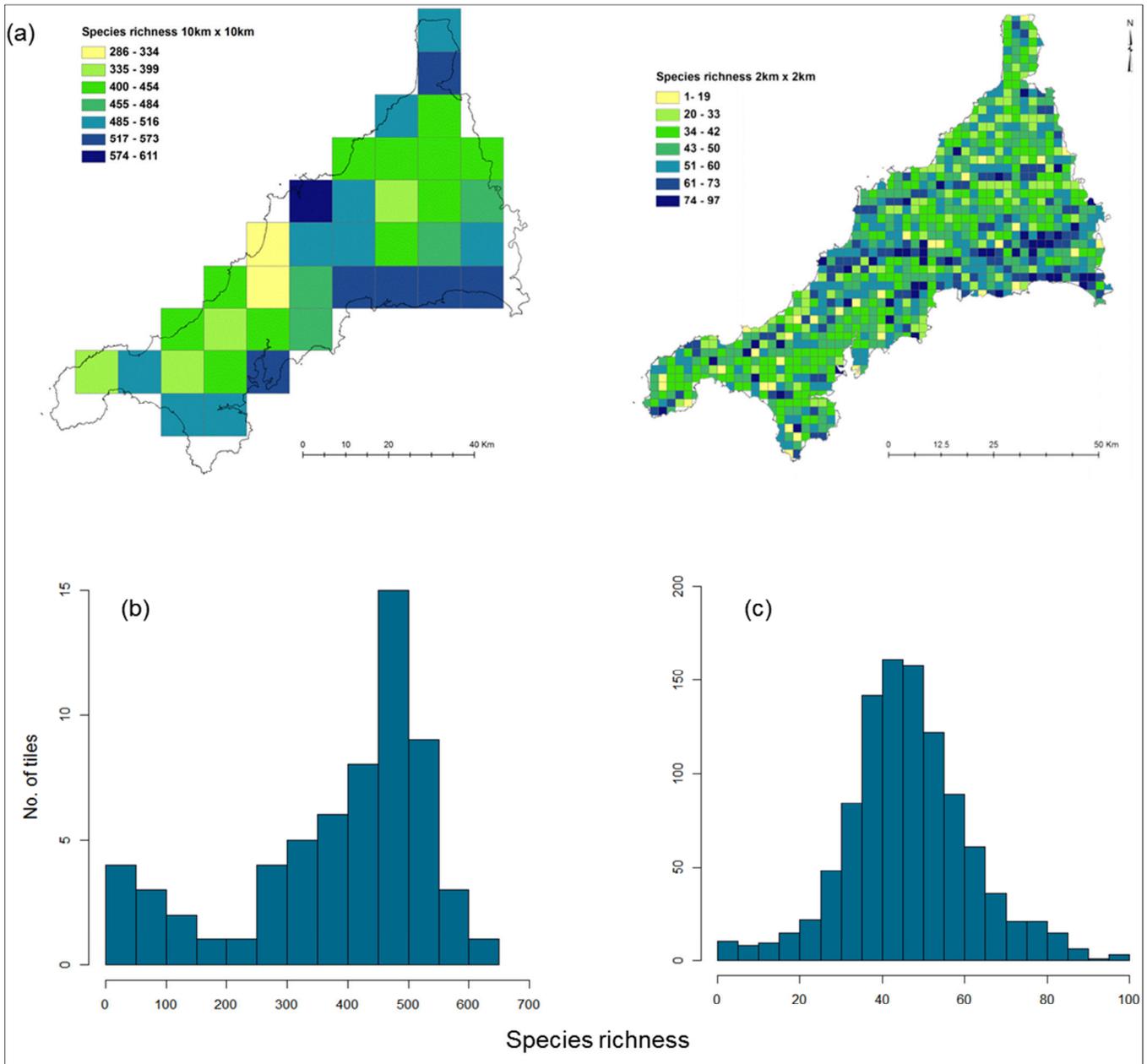
Figure 5. (a) Maps of the distribution of plant species richness in Cornwall at two different resolutions, and its frequency distribution in (b) at hectads (10x10km^2) and (c) tetrads (4x4km^2).
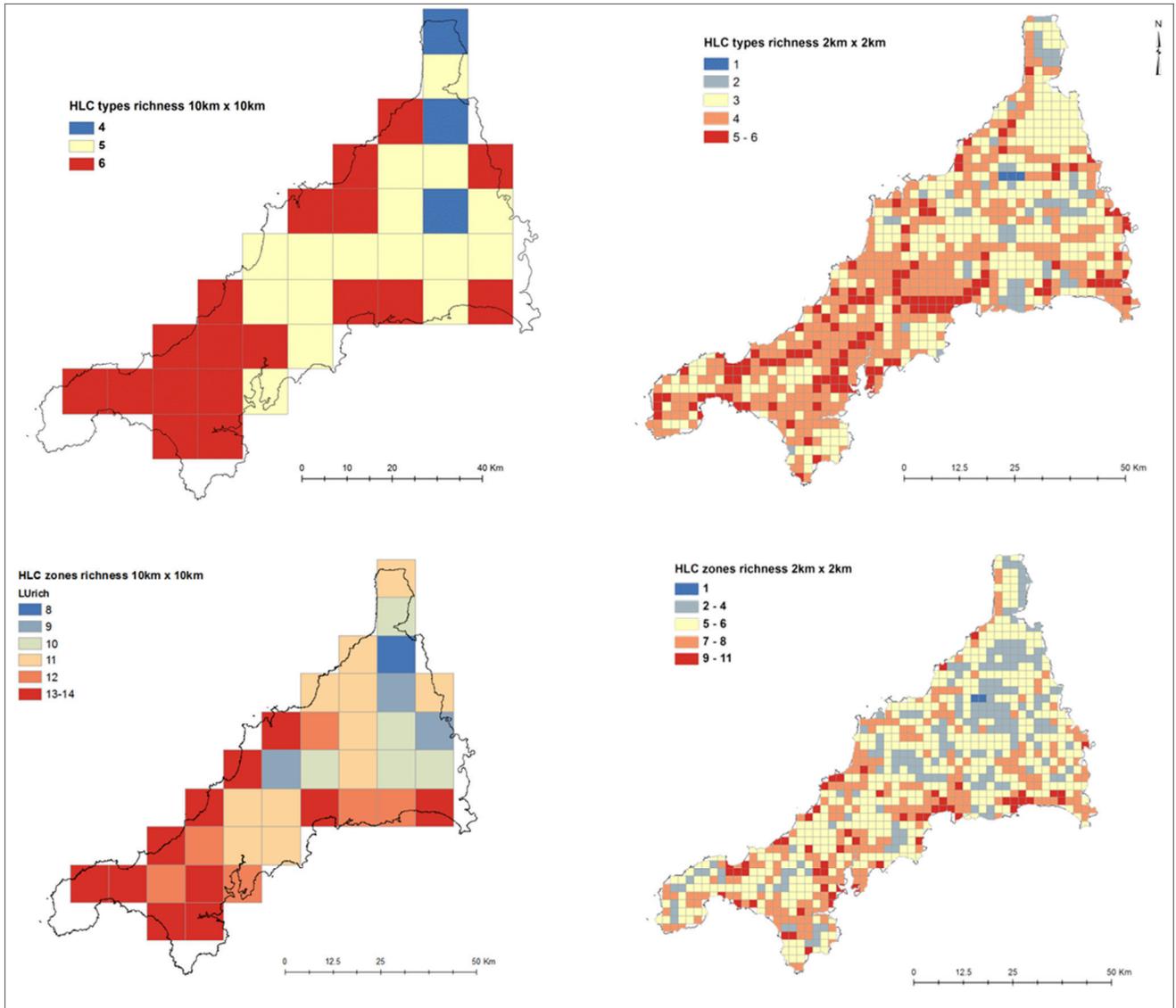
Figure 6 Map of the number of HLC merged types and HLC-zones for hectads and tetrads in Cornwall.

CHAPTER 5

Continuing exploring valuable data sets for plants, in this chapter I consider one of the most remarkable plant families in the arid lands of the Americas: the Cactaceae. Exploiting the availability of global range maps for virtually all of the extant species, one of the few plant groups for which these have been produced, I use this as a case study to determine the extent of a relatively new anthropogenic activity, artificial light at night, in relation to the distribution ranges of species.

Maria Eugenia Correa-Cano, Barbara Goettsch, James P. Duffy, Jonathan Bennie, Richard Inger and Kevin J. Gaston. **Erosion of natural darkness in the geographic ranges of cacti**. *In prep*.

Authors' contributions:

Conceived and design: MEC-C,KJG

Data provision: BG

Data analysis: MEC-C, JPD, JB

Draft chapter: MEC-C

All authors contributed equal to review the manuscript.

EROSION OF NATURAL DARKNESS IN THE GEOGRAPHIC RANGES OF CACTI

ABSTRACT

Naturally dark nighttime environments are being widely eroded by the introduction of artificial light at night (ALAN). The biological impacts vary with the intensity and spectrum of ALAN, but marked effects have been documented across multiple levels of organization, from molecules to ecosystems. How globally severe these impacts are likely to be depends in large part on the relationship between the spatio-temporal distribution of ALAN and that of the geographic ranges of species. Here, we define this relationship for an entire family of plants, the Cactaceae, determining how many species are experiencing ALAN somewhere in their geographic range, how extensive this influence is, how it changes with the size of the geographic range, how the distribution of ALAN interacts with that of species richness, and how all of these patterns are changing with shifts in levels of ALAN. We found that a high percentage of cactus species were experiencing ALAN within their ranges in 1992 (80%), and that this percentage had increased by 2012 (89.7%). For almost all cactus species (89.7%) the percentage of their geographic range that was lit increased from 1992-1996 to 2008-2012, often markedly. There was a significant negative relationship between both the species richness of an area, and that of threatened species, with the level of ALAN. Cacti could be particularly sensitive to this widespread and ongoing intrusion of ALAN into their geographic ranges, particularly when considering the potential for additive and

synergistic interactions with the impacts of habitat fragmentation, climate change, and other anthropogenic pressures.

INTRODUCTION

Concern is being widely expressed as to the negative environmental implications of the introduction of artificial light at night (ALAN), through the use of electric lighting (including, but not limited to, street lighting; Longcore and Rich 2004, Hölker et al. 2010a and b, Gaston et al. 2012, 2014). The reasons are twofold. First, ALAN has rapidly become extremely widespread (Cinzano et al. 2001, Gaston et al. 2014), continues to spread at a fast rate (Holker et al. 2010), and is increasingly taking more problematic forms (e.g. the progressive shift from narrow to broad spectrum lighting; Falchi et al. 2011). Second, empirical studies have demonstrated biological impacts of ALAN from the molecular to the ecosystem level (Gaston et al. 2013). Effects have been identified on the physiology, behavior, reproductive success and mortality of a wide range of species (e.g. Crawford 1981, Rand et al. 1997, Navara and Nelson 2007, Lacoeuilhe et al. 2014), on their abundance and distribution (Gaston and Bennie 2014), and in turn on community structures (e.g. Davies et al. 2012). Although substantially less attention has been paid to the impacts of ALAN on plants than on animals, direct effects have been demonstrated on plant productivity and phenology (Cathay and Campbell 1975a and b, Briggs 2006). In addition, indirect effects on plants can plainly occur through effects of ALAN on animals and their patterns of herbivory, pollination and seed dispersal (e.g. Bertin and Willson 1980, Macgregor 2014).

What has largely been missing from discussion to date of the impacts of ALAN has been an understanding of the proportion, and location, of species that are likely to be affected (Gaston et al. 2014). The first step here is to determine the relationship between the occurrence of, and trends in, ALAN and that of the geographic ranges of species in particular taxonomic groups. Key questions include how many species are experiencing ALAN somewhere in their geographic range, how extensive this influence is, how it changes with the size of the geographic range, how the distribution of ALAN interacts with that of species richness, and how all of these patterns are changing with changes in the levels of ALAN. To date, the only attempt to address these issues has been for terrestrial mammals, which revealed that most species are experiencing ALAN in some part of their geographic range, that in the majority of cases ALAN is increasing, and that ALAN may contribute to the patterns of risk of extinction of species (Bennie et al. 2014a, Duffy et al. 2015). Studies of many other taxa are plainly required however before any general conclusions can be drawn. Amongst plants this is challenging given the paucity of taxonomic groups for which global geographic ranges have been mapped for all or most of the species.

Here, we address the above questions about the relationship between the occurrence of, and trends in, ALAN and that of the geographic ranges of species, using the morphologically heterogeneous family Cactaceae (the cacti) as a case study. Unusually for a diverse (c.1500 species; Hunt et al. 2006) plant taxon, the global geographic ranges for the vast majority of extant species of cacti have recently been mapped as part of an assessment of their conservation status, and their threat status and use by people have also been determined (Goettsch et al. 2015). The group is of

particular interest for several reasons. First, naturally distributed almost entirely on the American continent (with the exception of *Rhipsalis baccifera*; Fig. 1), the family occurs across a wide range of climatic and ecological conditions (Oldfield 1997), and it is somewhat emblematic of, and predominantly distributed in, arid lands. Globally, these ecosystems have been shown to be disproportionately influenced by ALAN (Bennie et al. 2015). Second, the group has significant socioeconomic and cultural importance, with 57% of all known cactus species being utilized by people (Goettsch et al. 2015), and managed in wild and in anthropogenic created spaces (e.g. agricultural lands, pasture, and backyards; Casas et al. 1997, 1999, 2001). Third, cacti are amongst the most threatened of any species-rich taxonomic groups (animal or plant) to have been formally assessed to date, with the predominant documented threat processes being land conversion to agriculture and aquaculture, harvesting from the wild and, notably in the present context, residential and commercial development (Goettsch et al. 2015). Finally, there is evidence to suggest that ALAN might have an array of both direct and indirect effects on cacti (see Discussion). Direct effects include influences on germination and on time of seed quiescence (Rojas-Aréchiga and Vázquez-Yañes 2000). Indirect effects of particular concern are those of ALAN on pollinators and dispersers (e.g. bats and insects; Valiente-Banuet et al. 2004).

METHODS

Data

ALAN data were derived from the global nighttime light composite images from the Defense Meteorological Satellite Program's Operational Linescan System (DMSP-OLS), which currently provides the only available global scale long time series data suitable for analysis of the changing trends in ALAN. These images (available from www.ngdc.noaa.gov/eog/download.html) are annual cloud-free composites of detectable stable light sources on Earth. They are produced at ~1km resolution (resampled from data at 2.7km resolution) for the years 1992-2012. Each pixel value is represented by a digital number (DN) of between zero and 63. A value of zero represents darkness, while very brightly lit urban areas typically saturate at 63. Images used in this work were inter-calibrated (i.e. the brightness of images was cross calibrated due to the lack of on-board calibration of the sensor and the fact that the images include data from six different satellites) and drift-corrected (resolving geolocation errors) following Bennie et al. (2014b).

Data on almost all known cactus species were obtained from the Global Cactus Assessment (GCA; Goettsch et al. 2015). During this exercise, following a standardized IUCN methodology, the world's leading experts compiled data for each extant species on its distribution, population trends, habitat, ecology and threats, and evaluated its conservation status. All data collated during the assessment process are publicly available on the IUCN Red List website (http://www.iucnredlist.org/). The present work is based on the 1,435 cactus species for which range maps are available (of a total of 1,480). Rasterized maps resolution is 8.87 x 8.87 km (Goettsch et al. 2015 supplementary information). Following the GCA, we distinguished between those cacti that are utilized by people and those that are not, particularly as it seems likely that the

former are differentially exposed to ALAN (assuming a closer proximity on average to sources of artificial light). We included 10 broad categories of use: construction, animal food, human food, fuel, handicrafts, medicine (human and veterinary), other household goods, horticulture, specimen collection and other.

Data Processing

General trends

All data were re-projected to the Behrmann equal-area projection to perform analyses. Averaged intercalibrated DMSP images were calculated for the first five years (1992 - 1996) and for the last five years (2008-2012) of the time series using the DN values. We then extracted the DN values within the geographic range of each cactus species for the whole time series and for the two periods separately. The average intercalibrated DN value was also calculated for each species for all years.

Following Gaston et al. (2015), we defined a threshold for 'darkness' of less than 5.5 DN. This threshold was established after the finding by Bennie et al. (2014) that 94% of observed increases in DN of more than 3DN and over 93% of observed decreases of the same magnitude could be attributed to a known change on the ground consistent with the direction of change (i.e., urban expansion, industrial closure). The threshold of <5.5DN (or <6DN as a round value) is effectively twice the detection limit for change in DN, and thus provides a conservative estimate of the extent of ALAN due to noise in the data set or calculation errors (Gaston et al. 2015). The extent of ALAN found within the geographic range of individual species was assessed by calculating the

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proportion of lit pixels (the number of lit pixels/total number of pixels). In addition, two integrated cacti distribution maps were created: 1) a species richness map and 2) a threatened species richness map. Then, for both, each richness class was in turn subdivided (i.e. one raster created for each class) and used as a mask on the averaged DMSP image for the last five years (2008-2012). From the species richness map we obtained 82 different images, i.e. richness areas ranking from 1 to 82. We analysed 417 threatened species, each categorized by Goettsch et al. (2015) under one of the IUCN threatened categories: Critically Endangered, Endangered or Vulnerable (IUCN, 2001). For the threatened species richness map we obtained 14 different images, which correspond to each richness areas ranking from 1 to 14. Pearson's product moment correlation was determined for the relationship between species richness and the averaged DN values from 2008-2012. Threatened species richness was tested in the same way.

We tested whether an upward or downward trend in ALAN was occurring in the geographic ranges of each of the 1,435 cactus species for the entire time period (21 years) by applying a Mann-Kendall trend analysis. This is a test for monotonic trend in a time series based on the Kendall rank correlation and tau (McLeod 2014). The evenness of the nighttime light composite within the geographic range of each species was measured by examining the proportion of total pixels that contributed to 95% of the cumulative DN found within them (Σ DNs).

To evaluate whether there was a significant difference in the amount of ALAN in the geographic ranges of cacti that are used by people compared with those that are not, we applied a general linear model with the proportion of lit pixels (calculated as the

number of lit pixels averaged for the period 2008-2012 and then divided by the total range size per each species) as the dependent variable and a single fixed factor describing if the species was used or not. The proportion of lit pixels was arcsine square root transformed before analysis.

All data processing was performed using the statistical package R (R core team, 2014). Raster images were analysed using the packages 'raster' (Hijmans et al. 2014) and 'rgdal' (Bivand et al. 2015). The trend test was performed using the 'MannKendall' function implemented in the Kendall package (McLeod 2014).

RESULTS

Of the 1,435 species analysed, a high percentage (80.7%) had some areas of detectable ALAN within the bounds of their geographic ranges in 1992. This increased to 89.7% of species in 2012 (Table 1). In both years the geographic ranges of species between 1 – 567 pixels (relatively small) were lit throughout,, i.e. every pixel within their range had DN values ≥5.5 (0.6% of species in 1992 and 1.6% of species in 2012, Table 1). The spread of ALAN in these two time periods can be indirectly seen through the species with no lit pixels in their ranges, as in 1992 species with large distribution areas were under the threshold of darkness but in 2012 large ranges no longer appeared as entirely dark (Table 1). The overall trend of increasing erosion of natural darkness across the geographic ranges of cacti was apparent when comparing the percentages of their geographic ranges that were lit in different periods (Fig. 2). During 1992-1996 more than 800 species were experiencing ALAN across, on average, less than 5% of

their range. By 2008-2012 the number of species experiencing the same percentage of light across their ranges declined to nearly 600 species (Fig. 2).

Unsurprisingly, those species with geographic ranges with detectable levels of ALAN throughout had small geographic ranges (from 1-25 pixels), although some species with small geographic ranges had no detectable levels of ALAN (Fig. 3). For example, the range of *Cleistocactus pycnacanthus* (16 pixels) was lit throughout, whilst that of *Turbinicarpus alonsoi* was not lit at all (Fig. 3). Overall, there was a triangular relationship between the percentage of the range of a species that was lit and its range size, with some species across the breadth of range sizes being largely untouched by ALAN, and the maximal percentage of the range that was lit declining as ranges increased in size (Fig. 3).

For almost all cactus species the percentage of their geographic range that was lit increased from 1992-1996 to 2008-2012, often markedly (e.g. *Leptocereus leonii*, Fig. 4). Indeed, this percentage only declined for 10 species (*Echinocactus grusonii, Echinocereus barthelowanus, Escobaria_hesteri, Escobaria minima, Hylocereus extensus, Parodia buiningii, Parodia neohorstii, Sclerocactus nyensis,* and *Yavia cryptocarpa*). The decrease for *E. grusonii* could be explained by the fact that most of its range was converted into a dam in 1993, and therefore urban expansion and road development were stopped in the area. The area where *Echinocereus barthelowanus* grows was subject to mining activities, which apparently stopped during 2008-2012 or decreased its activities. For the other species we do not know the causes. The average number of lit pixels for all cactus species during 1992-2012, calculated by considering the average number of lit pixels for all the species in each of the 21 years, showed an

overall upward trend (Fig. 5a). This was confirmed by testing each species individually. For 1,186 cacti, the Mann-Kendall trend test gave positive tau values ranging from 0.31 to 0.85 (p = 1.19×10^{-7} to <0.05, n=1,435; Fig. 5b). A significant downward trend was found for three species: *Echinocactus grusonii* (tau=-0.64, p-value<0.001), *Sclerocactus nyensis* (tau=-0.43, p-value=0.007), and *Escobaria minima* (tau=-0.32, p-value=0.04). For a further 246 species there was no statistically significant temporal trend.

For the majority of species, a greater proportion of the geographic range contributed to 95% of the cumulative DN values when averaged over the last five years of the time series compared to the first five years (Fig. 6).

There was a significant negative relationship between the species richness of an area and its DN value for the first (1992-1996; rho= -0.21, 95% C.I: -0.24 to -0.17; p-value < 0.001) and for the last five years (2008-2012; rho= -0.19; 95% C.I: -0.22 to -0.16; p-value < 0.001) of DMSP-OLS data analysed. A similar relationship was found for threatened species richness for both periods (1992-1996, rho=-0.16, 95% C.I: -0.24 to -0.1, p-value<0.001; and for 2008-2012, rho= -0.2, 95% C.I: -0.21 to -0.06; p-value<0.001).

Cactus species that are used had a significantly higher proportion of lit pixels in their geographic ranges than did those that are not used ($F_{(1,1432)}$=6.23, p-value=0.01, Fig. 7).

DISCUSSION

Here we show for the first time the extent to which ALAN is co-occurring with the global distribution of a whole family of plant species: the Cactaceae. We further demonstrate that ALAN has increased in recent decades, both in terms of the number of species whose geographic ranges are overlapped and also in terms of the proportion of those ranges that are becoming brighter at night. Indeed, our results show that the vast majority of cacti (89.7%) had parts of their ranges already experiencing ALAN in 2012. This is a higher percentage than documented for mammals, which amongst vertebrates are of particular concern with regard to ALAN, given the prominence of nocturnal species in the group and the high level of extinction risk that many of them already face (Duffy et al. 2015).

Whilst based on the best data available, the analyses presented may actually underestimate the extent to which natural darkness has been eroded in the geographic ranges of cacti and the potential impacts. First, although the species range data are quite coarse relative to the ALAN data, potentially inflating observed levels of overlap between the two, this effect is likely to be outweighed by the fact that a conservative detection threshold was used for ALAN (see Methods) and that the ALAN data do not capture the full extent of skyglow, which may propagate emissions very far from the source (e.g. Biggs et al. 2012); maps of skyglow are not presently available. This may result in a substantial underestimate of the overlap. Second, ALAN rarely acts as an anthropogenic pressure in isolation, but is likely to act in additive and synergistic ways with an array of such pressures, including habitat fragmentation, climate change and chemical pollution (Gaston et al. 2014).

ALAN could have both positive and negative effects on cacti. The light requirements for successful germination, growth, fertilization and dispersal of plant species in general vary greatly. This is no less true of cacti, providing opportunities for ALAN to have diverse impacts. For example, early work performed by Alcorn and Kurtz (1959) on *Carnegiea gigantea* revealed that germination of seeds exposed to red and far-red light in a lighted room was higher than under dark conditions, presenting evidence of germination of light-sensitive seeds. Zimmer (1969) reported that some cactus species germinate in the dark (*Mammillaria longimamma*, *Helianthocereus pasacana*), while others require long exposure to light (*Parodia maassii*). More recent studies have sustained the importance of light and/or darkness for germination (Rojas-Aréchiga et al. 1997; see Rojas-Aréchiga and Vázquez-Yañes 2000 for a review, De la Barrera and Nobel 2003). The requirement for light to trigger the interruption of seed quiescence provides competitive advantages in diverse species and can be a determinant of the structure of plant communities (Vázquez-Yañez and Orozco-Segovia, 1990, 1996; Baskin and Baskin, 1998; Restrepo and Vargas, 1999). These experiments although not focused on determining the effect of light pollution on seed germination highlight the variation of light requirements to trigger germination across species. ALAN might alter plant community composition by changing differentially germination rates across species.

Cacti have crassulacean acid metabolism (CAM) which enables plants to improve water efficiency by opening stomata at night and keeping them closed during the day, the hot and drier period. Although there is no direct published evidence that ALAN can have an effect on the CAM process, the amount of light received by CAM

plants has an effect on the opening of stomata (Nobel and Hartsock 1983), affecting the balance between CO_2 fixation and the accumulation of organic acids (Nobel 1981, Lüttge 2004). Exposure to ALAN by cactus species might induce an extension of the time for which stomata are closed, triggering a less efficient CO_2 fixation. CAMs contribution to total CO_2 fixation depends on many factors, from differences in genotypic expression to variable environmental conditions (Cushman 2001, Keeley and Rundel 2003), and disentangling the effect that ALAN may have on this process is not an easy task.

ALAN is likely also to have indirect effects on cacti, including via impacts on pollinators and dispersers. Pollinators of cacti include insects, birds and bats (Valiente-Banuet et al. 2004), all groups whose behavior has been shown to be vulnerable to influences by ALAN (e.g. Longcore, 2010, Somers-Yates et al. 2013, Lacoeuilhe et al. 2014, Lewanzik and Voigt 2014). Valiente-Banuet et al. (2004) and Valiente-Banuet et al. (1996, 2002) report that the majority (72%) of species of columnar cacti (Tribe Pachycereeae) found in Mexico (70 species) are bat pollinated. Valiente-Banuet and Arizmendi (1997) also recognized two main groups of dispersers of cacti. Primary dispersers take fruits directly from the plant during the day (e.g. birds, lizards) and night (e.g. bats); more generally, the behavior of bats has been shown almost invariably to be influenced by ALAN. Stone et al. (2009) showed that the activity of lesser horseshoe bats (*Rhinolophus hipposideros)* was significantly delayed in the presence of lighting (illuminated on average under 53.09 lux). Lacoeuilhe et al. (2014) identified two groups of bats, one that was light-tolerant and a second group that was light-intolerant (under an illumination range between 0 and 25 lux). We can infer that, most bat species might

be affected by the introduction of ALAN in their commuting or feeding areas, and those effects might ultimately alter plant species abundance and distribution where plants depend on bats for pollination. Evidence of the effects of changes in the abundance and migration routes of the long nose bat *Leptonycteris yerbabuenae* can markedly affect gene flow dynamics in the columnar cacti *Stenocereous thurberi* which the bat pollinates (Bustamante et al. 2016).

Secondary dispersers take the fruits from the ground (e.g. ants and rodents), and again are likely often to be nocturnal; rodent behavior has been shown often to be strongly shaped by ALAN (Gaston et al. 2013). Empirical observations of the lesser long-nosed bat (*Leptonycteris curasoae*), a species that pollinates columnar cacti, have shown that it prefers environments with lower light intensities for foraging movements (Lowery et al. 2009), avoiding lit areas to avoid be visible to predators (Fleming, 1988). Alterations on the behavior of *Leptonicteris curasoe* due to ALAN might cause changes in cacti at individual and/or community level if for example; individuals of cactus species nearby lit areas are avoided by bats, altering pollination and dispersion at individual level and in a long term, modifying community composition. Disruption or alteration of nocturnal rodent's behaviour may lead to an alteration of ecological interactions, triggering a chain of events at community level. For example, if for a given nocturnal rodent species onset and end of activities are postulated due to ALAN, individuals might be exposed to different rates of predation, and/or being out of step with food sources due to changes in competitive interactions. Modification of these ecological interactions might change indirectly dispersion of cactus species.

ALAN and new lighting technologies are transforming landscapes at night by increasing brightness and adding a broader spectrum of light (Gaston et al. 2013). Unfortunately, there is no single measure of light intensity that is suitable for quantifying the varying physiological effects of ALAN on plants (Bennie et al. 2016). In the present study, we analysed values taken remotely from satellites, which have been analysed and averaged to produce composite images of ALAN. Although highly valuable, it is not possible to transform between DN values and other units used to measure light pollution (e.g. illuminance given in lux). Nevertheless, for the purpose of comparison, it is important to consider that the amount of artificial light at night often surpasses illumination from natural sources. For instance, the illumination of a full moon under clear conditions is estimated to be between 0.1 - 0.3 lux, while an artificially lit parking lot is c.10 lux (Bennie et al. 2016), and or skyglow within cities has been recorded at between 0.1 - 0.5 lux (Eisenbeis 2006). Additionally, illuminances measured in vegetation in the UK showed that the leaves of trees in the beam of a car headlight may be exposed to thousands of lux, while roadside vegetation directly beneath streetlights might experience around 50 lux (Bennie et al 2016, see Rich and Longcore 2006 and Gaston et al. 2013 for a comparison between variation in levels of illuminance between natural and artificial sources). This direct illumination added to the skyglow effect, may have diverse effects on species, ranging from physiological impacts to, in the long term, changes in species composition, altering ecosystems. Further studies on the effects of changes in illumination and spectral composition are necessary to determine the effects on cacti species and in general on plant species.

It remains challenging to discriminate the particular influences of ALAN on the distributions of species and on patterns of species richness from those of other factors that are commonly associated with the introduction of ALAN into the environment, especially habitat change. Nonetheless, the negative relationships documented between the species richness of cacti (and of threatened cacti) and levels of ALAN suggest that high levels of ALAN in an area may not be conducive to a high biodiversity of cacti.

Cacti are perceived as amongst the most charismatic of plant taxa, emblematic of arid lands, and of major cultural significance (Goettsch et al. 2015). They may thus be of particular concern in terms of the impacts of ALAN, especially given the high proportion of species experiencing the erosion of natural darkness within their geographic ranges. However, there is little reason to believe that such changes are atypical of those that are being experienced by many other groups of organisms.

TABLES

Table 1. The number of cactus species with lit pixels (DN≥5.5) in their geographic range, with no-detectable light in their range and only lit pixels in their range in 1992 and 2012, and the variation in the range sizes of the species in these different groups. Total number of cactus species analysed =1,435.

	Number of species		Range size (No. of pixels)	
	1992	**2012**	**1992**	**2012**
With lit pixels in their range	1,158	1,287	3 – 25,969,250	1 – 25,969,250
With no lit pixels in their range	278	149	1 - 118,348	1 - 16,681
With only lit pixels in their range	8	23	3 - 202	1 - 567

FIGURES
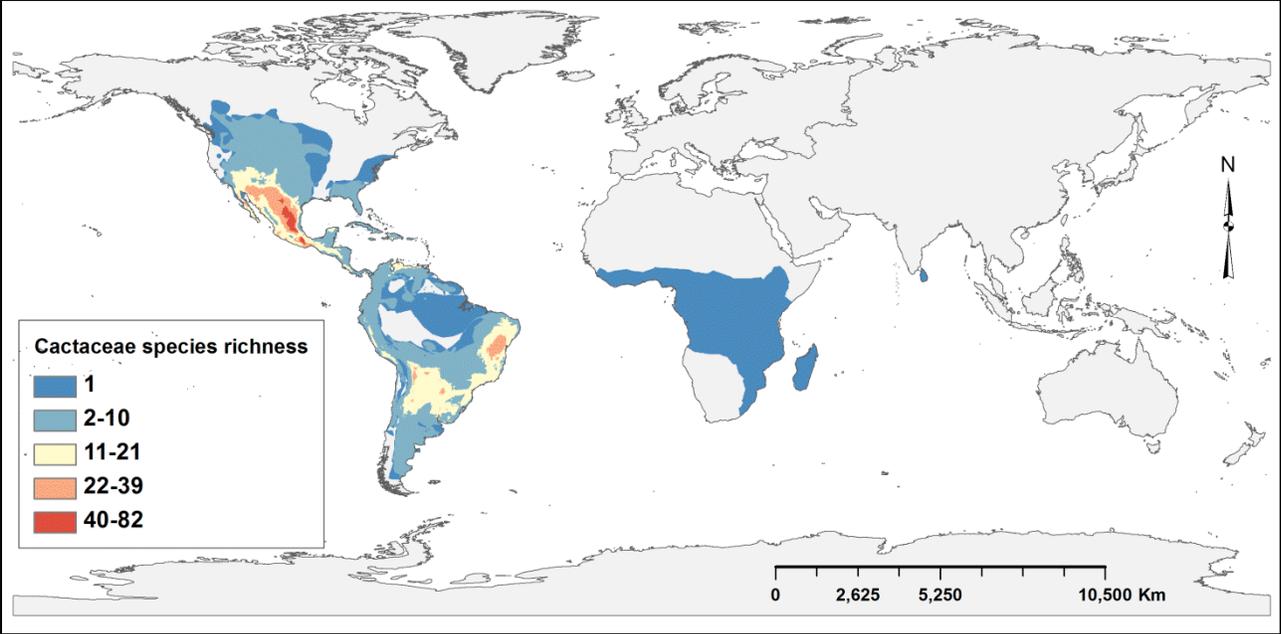
Figure 1. Geographic distribution of cactus species richness (Behrmann equal-area projection).
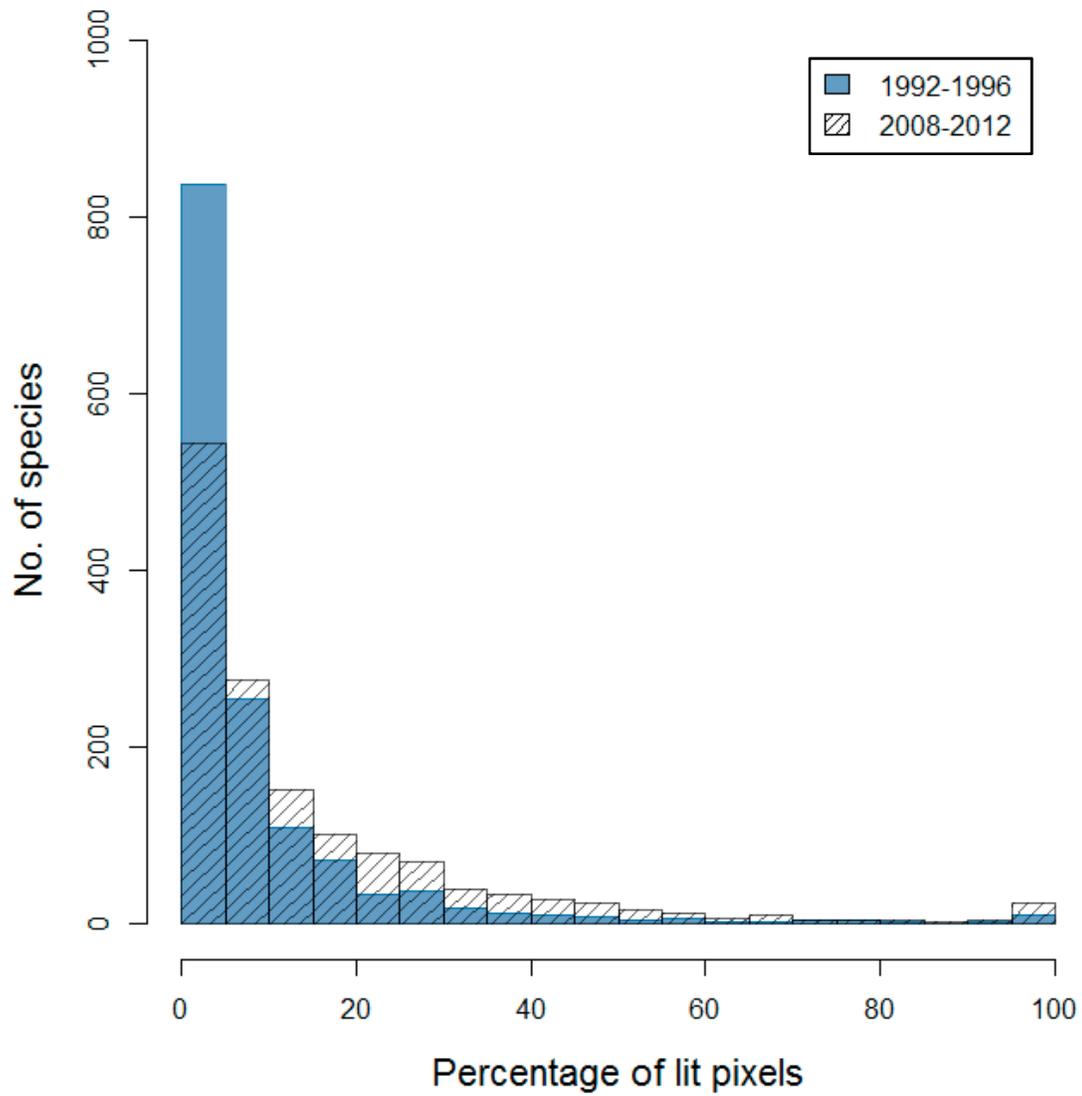
Figure 2. Frequency distribution of the numbers of cactus species with different percentages of their geographic ranges lit for the periods 1992-1996 and 2008-2012.
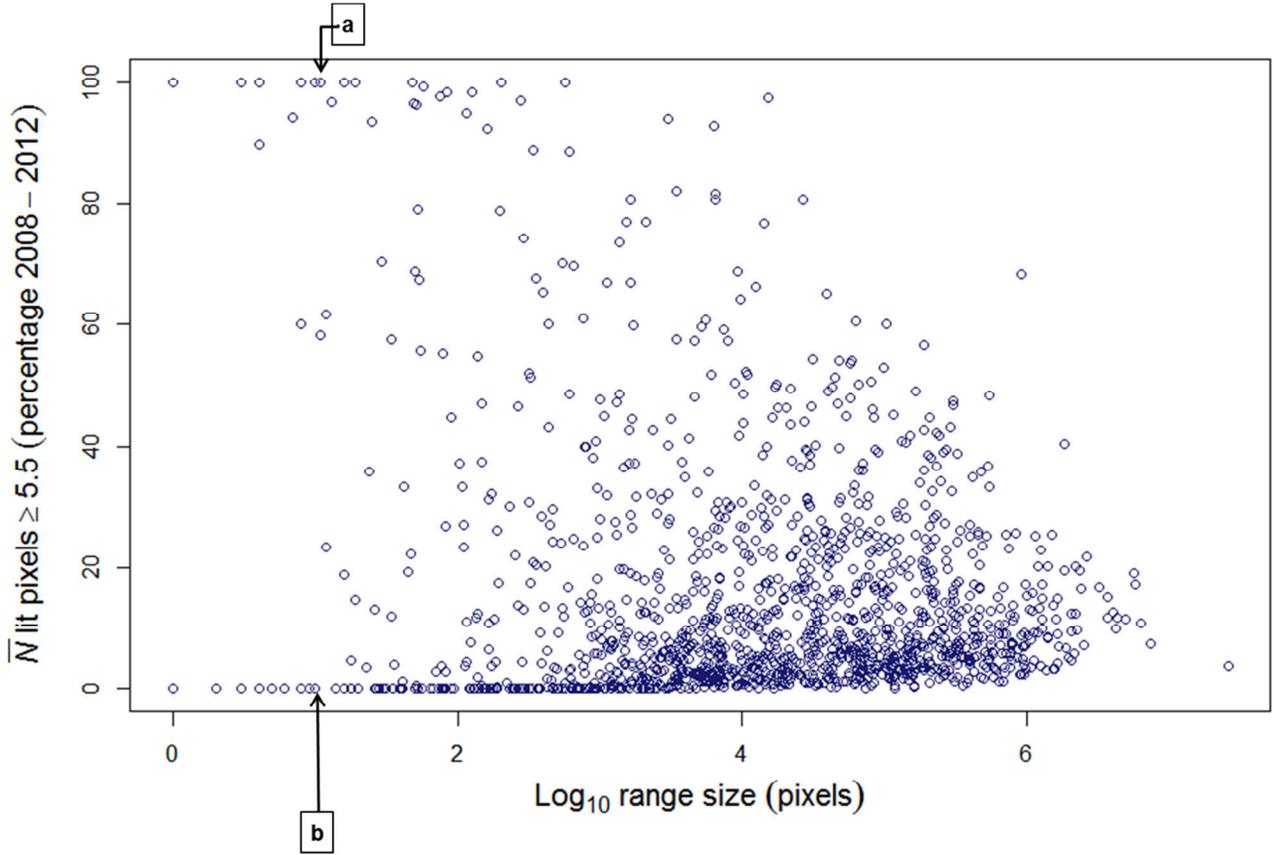
Figure 3. The relationship between the average percentage of the range of each cactus species ($\overline{N}$) that was lit in 2008-2012 and its range size. Species with similar small range sizes a) *Cleistocactus pycnacanthus* and b) *Turbinicarpus alonsoi*.
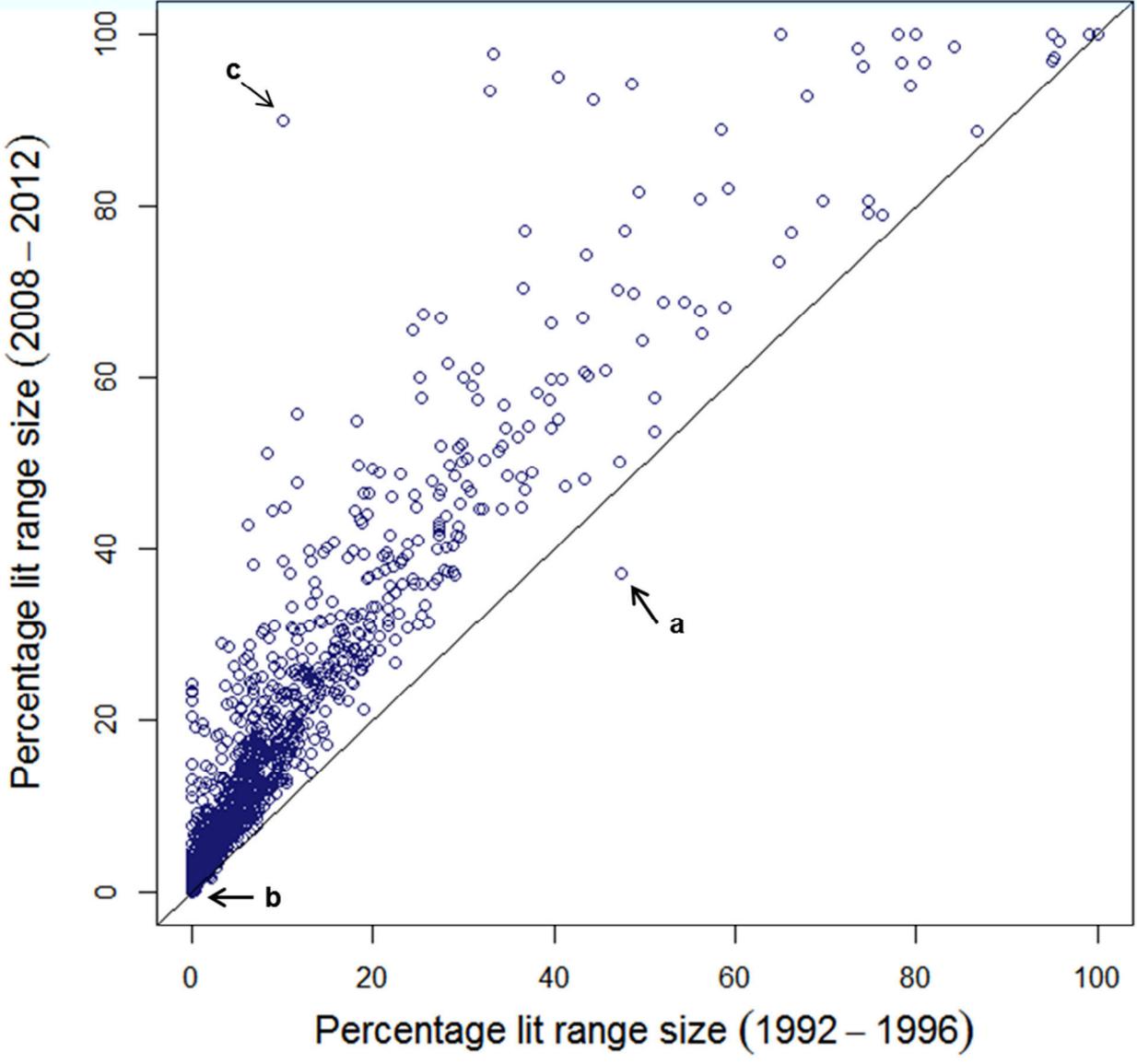
Figure 4. The relationship between the percentage of the geographic range of each cactus species that was lit in 1992-1996 and in 2008-2012. The solid line is that of equality. (a) *Echinocactus grusonii*,(b) *Sclerocactus nyensis* and c) *Leptocereus leonii.*
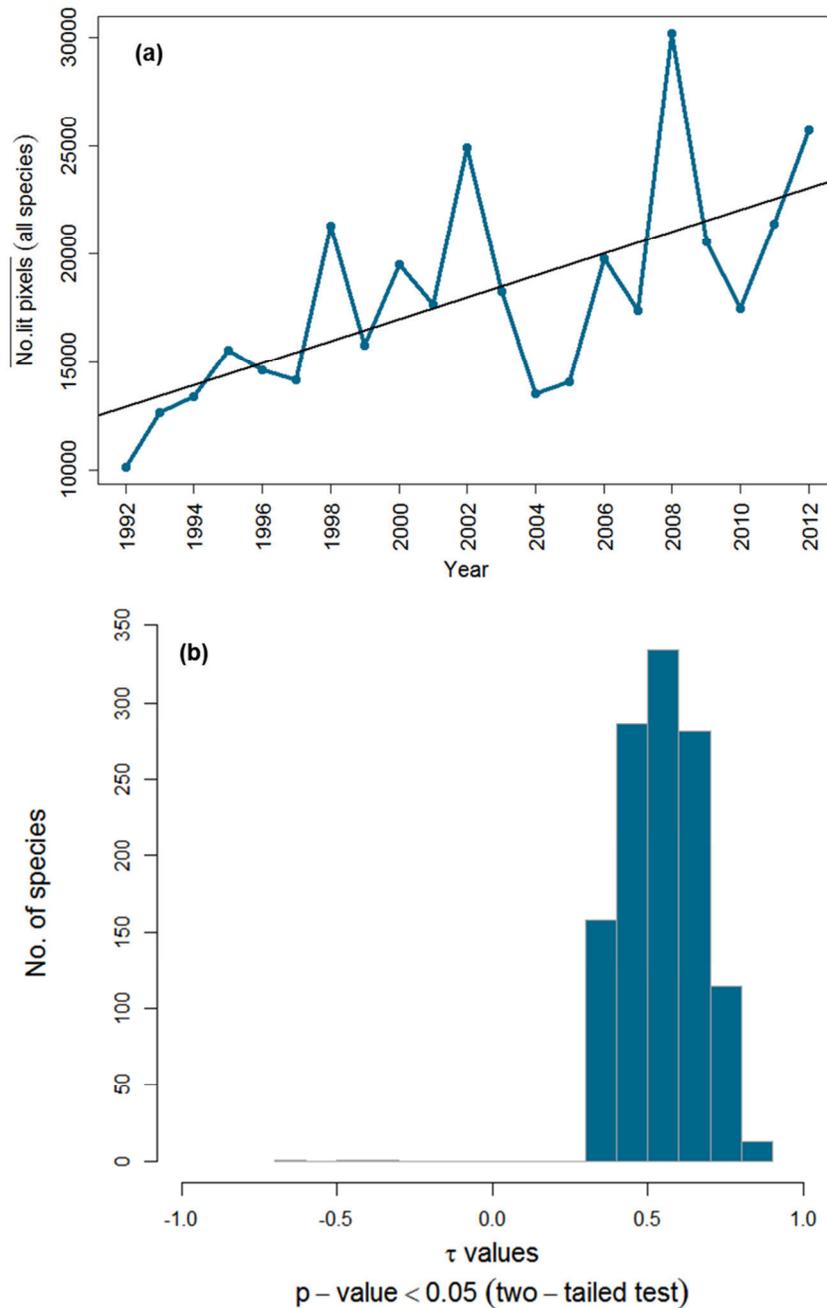
Figure 5. Trend of ALAN in ranges of cactus species. a) Temporal trend in the average number of lit pixels calculated across all cactus species during the 21 years; b) number of cactus species with significant positive (1,186 species) and negative tau values after performing a Mann-Kendall Trend Test. Significant negative tau values correspond to *Echinocactus grusonii* (tau=-0.64), *Sclerocactus nyensis* (tau=-0.43) and *Escobaria minima* (tau=-0.32).
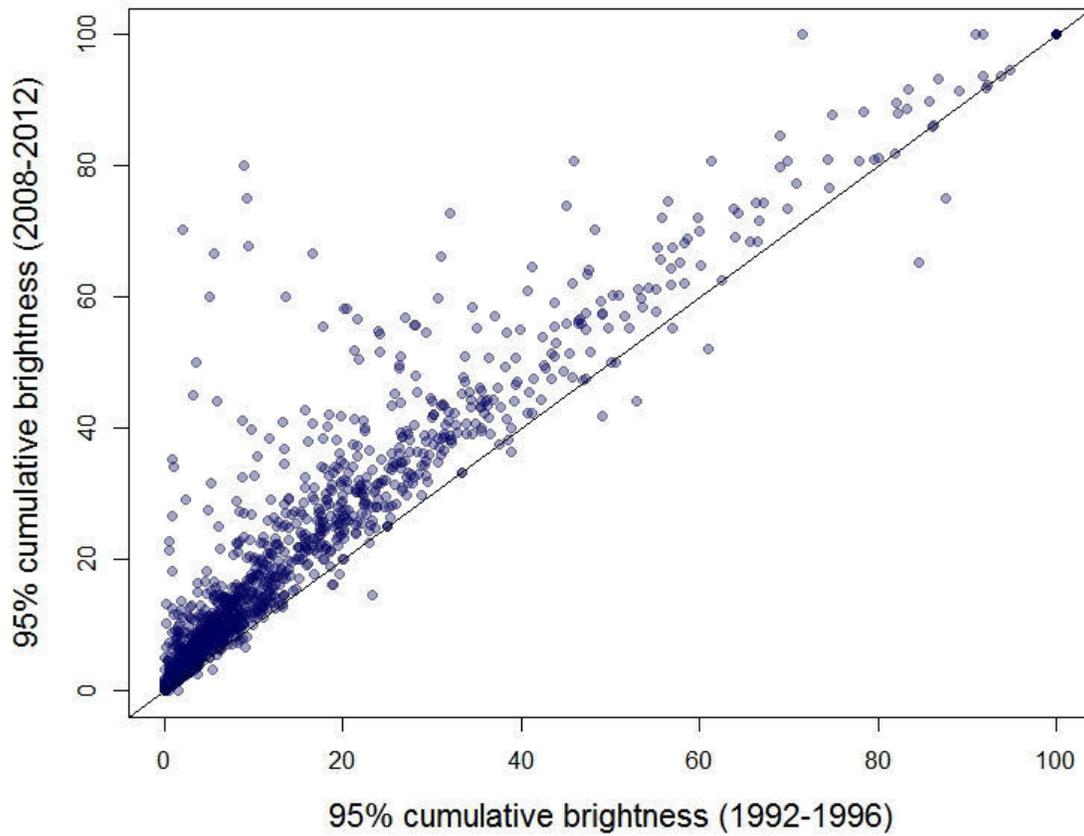
Figure 6. The relationship between the percentage of pixels contributing to 95% of the cumulative digital number (ΣDN) within the geographic range of each cactus species in 1992-1996 and 2008-2012. The line represents the 1:1.
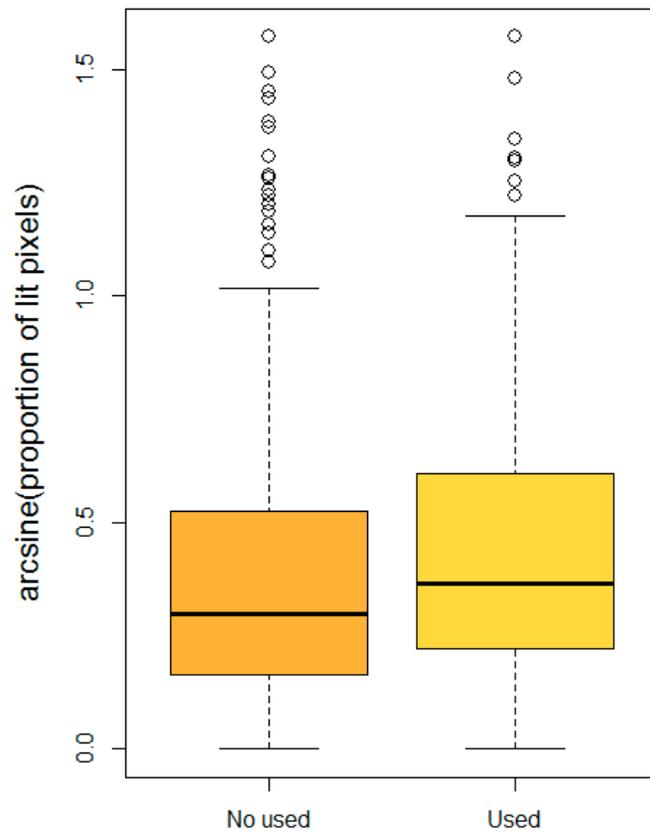
Figure 7. Average proportion of lit pixels for 2008-2012 (arcsine transformed) in the geographic ranges of cactus species that are (838 species) and are not used by people (597).

CHAPTER 6

In this sixth chapter I continue to explore the interaction between the distributions of species and of artificial light at night. As highlighted in chapter 5, a major constraint in so doing lies in the spatial resolution of the data that are available. Here I utilise some of the best data available in this regard, distribution data for the threatened plant species in Britain and new data on nighttime radiance from the SUOMI satellite.

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Authors' contributions:

Conceived and design: MECC, KJG

Data provision: KW

Analysis: MECC

Draft manuscript: MECC

RELATIONSHIP BETWEEN DISTRIBUTIONS OF THREATENED PLANTS AND ARTIFICIAL NIGHTTIME LIGHTING IN BRITAIN

ABSTRACT

Despite the depth of knowledge of the distribution of artificial nighttime lighting, and the undoubted range and intensity of its impacts on organisms, the degree of overlap between this lighting and the distributions of species remains surprisingly poorly understood. Here, we determine the finer scale relationship between the distribution of threatened plants in Britain and that of artificial nighttime lighting. In so doing, we exploit the existence both of an exemplary data set on the occurrence of species at fine spatial resolutions, and of new remote sensed imagery of nighttime lighting. The results showed that only 8% of Britain is dark at night, with 92% of the land cover lit to some degree by artificial light at night. In consequence, 10% to 100% of the distribution ranges of 200 threatened plant species is lit at night. There were no significant differences in the average radiance values for British CR, EN or VU species, with all having average radiance values of <4.3 nW/cm^2*sr, less than those found in villages or towns. There was a weak significant negative relationship between the average radiance and the extent of protected areas. Our results suggest that attention should be paid to the potential influences of artificial nighttime lighting on threatened plant species.

INTRODUCTION

Some of the most compelling visual images of the impacts of humankind on the natural environment are those of artificial nighttime lights taken from satellites or by astronauts (e.g. Cinzano et al 2001, Elvidge et al 2001, Elvidge et al. 2013, Davies et al. 2014, de Miguel et al. 2014). The extent and magnitude of this lighting is such that alone it is sufficient to enable the distribution of land masses to be discerned, sometimes in considerable detail, across much of the Earth. Resulting from a diversity of sources (e.g. streetlights, buildings, road vehicles, vessels) artificial nighttime lighting is especially prevalent across much of Western Europe. Recent analyses have documented ongoing increases in artificial nighttime lighting across the region (Bennie et al. 2014a). Indeed, across Europe about a quarter of all protected areas, which should arguably be amongst the least influenced parts of the region, have exhibited high levels of such lighting since at least the early 1990s, and nearly a third have experienced significant increases in that lighting in the period since (Gaston et al. 2015a).

A substantial evidence base now exists of the biological impacts of artificial nighttime lighting (Rich & Longcore 2006, Perkin et al. 2011, 2014, Gaston et al. 2013, 2015b). These influences range from gene expression through to community composition (Martino et al. 2004, Ishida et al. 2005, Queval et al. 2007, Fonken et al. 2010, Brei et al. 2014, Day et al. 2015, Davies et al. 2012, 2015). This includes impacts on microorganisms (Hays 2003, Cohen & Forward 2009), invertebrates (Frank 1988, Perkin et al. 2014, Moore et al. 2006, Hagen et al. 2015) and vertebrates (Buchanan 1993, Fraser and Metcalfe 1997, Lacoeuilhe et al. 2014, Gaston & Bennie 2014). Understanding of the impacts of artificial nighttime lighting also on plants has been

acquired much more slowly outside of the horticultural context, but there is evidence for effects on timings of bud burst, flowering and leaf abscission, on germination rates (Edward & El-Kassaby 1996), on levels of pollination (Rydin & Bolinder 2015), and on growth and herbivory (Kalka et al. 2008, Bennie et al. 2015, submitted). In turn, it is predicted that, as with other taxa, this will shape the abundance and occurrence of plant species (Figure 1), although the experiments being conducted to test such effects have yet to report their findings in these regards (Bennie et al. 2015).

Despite the depth of knowledge of the distribution of artificial nighttime lighting, and the undoubted range and intensity of its impacts on organisms, the degree of overlap between this lighting and the distributions of species remains surprisingly poorly understood. On the one hand, one might predict that whatever its effects, artificial nighttime lighting would influence a relatively small proportion of species, because the majority do not occur in the more heavily developed parts of the landscape in which lighting devices disproportionately occur. On the other hand, the documented extent of the spread of skyglow from urban centres (Biggs et al. 2012, Luginbuhl et al. 2014), and the reach of artificial nighttime lighting into many protected areas (Gaston et al. 2015a) suggests that it would be unwise to be complacent in this regard. The only attempts to date to determine the relationship between the distribution of species and that of artificial nighttime lighting have been conducted at global or continental scales, using relatively coarse resolution data (albeit the best available) on the distributions both of species and of lighting (Duffy et al. 2015, see Chapter 5). Whilst enabling broad patterns to be discerned, inevitably this overlooks the undoubted finer scale

heterogeneity of species occurrences and of lighting (e.g. Gaston 2003, Bennie et al. 2014b).

In this paper, we determine the finer scale relationship between the distribution of threatened plants in Britain and that of artificial nighttime lighting. In so doing, we exploit the existence both of an exemplary data set on the occurrence of species at fine spatial resolutions, and of new remote sensed imagery of nighttime lighting. We also determine the extent of nighttime lighting in protected areas in the region, given that a high proportion of the threatened plant species have previously been shown to occur within such areas (Jackson et al. 2009).

METHODS

Data

A nighttime light composite image was obtained from the NOAA National Centers for Environmental Information (formerly the National Geophysical Data Center, http://www.ngdc.noaa.gov/eog/viirs/download_monthly.html). This composite of the Earth at night was assembled from data acquired by the Suomi National Polar-Orbiting Partnership (Suomi NPP) satellite during May 2014 with data collected on nights with zero moonlight (Lee et al. 2006). The nighttime view of Earth was made possible by the day/night band (DNB) of the Visible Infrared Imaging Radiometer Suite (VIIRS). The DNB has a measured spectral response of 505-890nm, featuring several advances over the previous Operational Linescan System (OLS), including full calibration and improved spatial (0.74 km vs. ~3km) and radiometric (1-bit vs. 6-bit) resolutions (Miller et al 2013; Schueler et al. 2013). The data are at 750m resolution and each pixel is represented by

a DNB radiance value. The minimum detectable radiance is ~2×10^{-10} W·cm^2·sr^{-1} at nadir, with no saturation even with full solar illumination (Liao et al. 2013). Smaller radiance values, i.e. values close to zero, represent the average darkness in a month for a given area. All radiance values are given as floating points.

We analysed 101,123 records of threatened plant species for Great Britain (henceforth Britain); given limitations on the availability of strictly comparable data, it was not possible also to include Northern Ireland. Data were obtained directly from the Botanical Society of the British Isles. Only records from 1987 onwards were considered since the collection effort and the survey methodology are considered to be reasonably even for this period but not before. A total of 272 species categorised on the Vascular Plant Red List for Great Britain (Farrell 2005) as critically endangered (CR), endangered (EN), and vulnerable (VU) were included. Each species record was assigned to its respective 2km x 2km tetrad. Plant species analysed consisted of ferns, gymnosperms, and flowering plants, including subspecies, critical species, and microspecies (e.g. *Heiracia, Sorbus, Euphrasia*), hybrids, and some long established alien species (archaeophytes) with a long introduction to the UK (e.g. *Potamogeton epihydrus, Spergula arvensis*).

Two different sources of data on protected areas were used, the World Database of Protected Areas (WDPA) and the Joint Nature Conservation Committee (JNCC). Data from WDPA (IUCN-UNEP-WCMC) downloaded in May, 2015 contained a shapefile of Statutory Protected Areas (Local Nature Reserves, National Nature Reserves, Sites of Special Scientific Interest and Ramsar sites) and Protected Landscapes (Areas of Outstanding Natural Beauty and National Parks, Figure 2c). The

JNCC data set contained polygons of two categories of Statutory Protected Areas; Special Areas of Conservation, and Special Protection Areas (Figure 2c). The information was downloaded in March, 2015.

Processing

The following processes were performed in ArcMap ver.10 (ESRI 2011), unless otherwise specified. All data were re-projected to National Grid coordinates (OSGB 1936 British National Grid) using the 'gdalwarp' utility in GDAL tools (Geospatial Data Abstraction Library, http://www.gdal.org/). During the process, the nighttime lighting composite was re-sampled selecting a cubic option, which is appropriate for continuous data and it is geometrically less distorted than a raster achieved by running other resampling algorithms. After re-projecting and re-sampling, the effective cell size was 375.426 m x 375.426 m. Each radiance value (floating points) from each cell covering Britain was extracted to plot the distribution of lit pixel values (more than 1.6 million pixels). We added 1 to the rounded down data and log transformed the number of lit pixels within bins of ~12 nW/cm^2*sr width. Radiance values contained within the geographic range of each individual plant species were also extracted and its average considered independently. In addition, species richness in each tetrad was calculated, for species of each IUCN threat category. Nighttime lighting data values were extracted and averaged for each tetrad containing at least one plant species record.

All Protected Areas were combined and dissolved (to avoid overlapping polygons from different areas) to create a single layer. A separate layer was created in the same way representing Protected Landscapes. Both layers were transformed to raster files

before extracting the radiance values. All extractions and averaging calculations were carried out using 'extract by mask' and 'zonal statistics', respectively. All graphs were produced using R (2015).

The minimum detectable radiance is ~2×10^{-10} W·cm^2·sr^{-1} at nadir, however, the radiance values obtained from NOAA are values averaged in a month, therefore values close to zero represent the average darkness in a month for a given area. Here, we consider a threshold for 'darkness' with radiance values equals zero. Note that the SI unit of radiance is the watt per steradian per square metre per hertz (W·cm^2·sr^{-1}); which differs from the DN or digital numbers considered in Chapter 5.

RESULTS

Measured nighttime light values across Britain ranged from zero, representing darkness, to 609.2 nW/cm^2*sr, observed in Teesmouth, Nr Middlesbrough (Figures 2a and 3). Considering darkness (or at least values below the detection threshold of the instrument) to be represented by values of zero, only 8.08% of Britain appeared to be dark, however, 68% of all pixels covering Britain had radiance values between 0.000001 and 1.005 nW/cm^2*sr, i.e. radiance values close to darkness. The brightest areas were located in cities, e.g. Manchester and Soho, London showed radiance values of 198.14 and 190.38 nW/cm^2*sr respectively. In contrast, dark areas were often found in protected landscapes, e.g. Cairngorms National Park, and North Dartmoor had average radiance values of zero (Figure 3A).

A large number of threatened species had some parts of their distribution ranges overlapped with non-zero radiance (Figure 4). 200 species had from 10% to 100% of their ranges overlapped with non-zero radiance values at night (Figure 4a), and only approximately 70 species had 5% or less of their ranges overlapped with some positive value of radiance. The relationship between the percentage of the geographic range of each species that was lit and its range size was approximately triangular (Figure 4b). Larger geographic ranges tended to have a lower percentage of lit pixels than smaller ranges; however some species with small geographic ranges had a small percentage of this area lit. The location of species ranges was important in determining the degree of overlap with radiance values.

For 109 species, around 40-60% of the total number of pixels covering their respective ranges accounted for 95% of the summed radiance values for those ranges, demonstrating that this lighting was relatively widespread through their ranges. Only for a few species (less than 5) was 95% of the cumulative radiance focussed within less than 40% of the pixels in their ranges (Figures 5a and b).

Although a high proportion of the species had pixels within their ranges with maximum radiance values higher than $50nW/cm^2$*sr (equivalent to values commonly found in towns), most of them also had pixels with minimum values at or below the threshold of darkness (less than $1nw/cm^2$*sr, Figure 6).

The radiance received by CR species (n=29) averaged 4.1±4.9 nW/cm^2*sr, contrasting with EN species (n=73) which received 2.35±2.4 nW/cm^2*sr and with VU species (n=170) with an average of 2.1±2.6 nW/cm^2*sr (Figure 7). However, there was

no significant difference in mean radiances values between IUCN categories ($F_{(2,65.54)}$=2.45, p=0.1).

Most of the threatened plant species ranges, had average radiance values of less than 10 nW/cm^{2}*sr (Figure 8c); radiance values of 10 nW/cm^{2}*sr were generally found in the immediate surrounding area of almost every city. Seven species ranges had average radiance values > 10 nW/cm^{2}*sr and no species range was found with average values higher than 25nW/cm^{2}*sr. These radiance values are found around the center of cities. Some species with very restricted distribution areas, such as *Epipactis sancta* (Figure 8a), *Diapensia lapponica,* and *Bupleurum baldense,* were under darkness (radiance values equal zero) throughout their range.

There was no significant relationship between the average radiance values per tetrad and species richness (b=-0.02, 95% CI: -0.005 to 0.002, R^2<0, $F_{(1,20248)}$=0.8), however the upper limit to radiance tended to decline with increasing species richness (Figure 9). 33% of the tetrads in Britain were occupied by threatened plant species. Of these, 54.24% were occupied by just a single species, i.e. ~15% of the total. These single-species tetrads had average radiance values ranging from 0 to 111.66 nW/cm^{2}*sr. 45.33% of tetrads contained between 2 and 10 species with average radiance value of 2.40 nW/cm^{2}*sr. However, the tetrad with the maximum radiance value (176.82 nW/cm^{2}*sr, Figure 9) was located at Coatham Sands, North Yorkshire, and contained four threatened species: *Astragalus danicus, Blysmus compressus, Chenopodium glaucum and Salsola kali* subs*. kali.* Only 0.42% of the tetrads with presence of threatened plants are high in species richness (11-20 species). The maximum radiance value over these reached 40.3 nW/ cm^{2}*sr in a tetrad containing 11

species, located at Portsmouth. The highest species richness tetrad (20 species) was located at Marsworth, Buckinghamshire with an average radiance value of 2.06 nW/cm^2*sr. Tetrads with high threatened species richness (11-20 species) were scarce and more likely to be covered on average by low radiance values (Figure 8 and 2b). In contrast, tetrads with low threatened species richness were abundant and had a similar probability of having either radiance values equal zero or higher than 50 nW/cm^2*sr, which is a radiance value found around Birmingham Town Hall, Birmingham for example.

There was a weak significant negative relationship between the average radiance values of a protected area and its size (b= -1.45, 95% CI: -1.7 to -1.2, R^2=0.02, F$_{(1,7290)}$=122.1, Figure 10). The relationship between the size of a protected area and its average radiance had a triangular shape. Larger areas were more likely to have small average radiance values than small areas. Small protected areas had a broad range of radiance within their extents, ranging from zero to 100 nW/cm^2*sr for the smallest areas.

221 protected areas (3.03%) were on average under darkness (radiance value of zero). 57% of protected areas had average radiance values between 0.1 and 1nW/cm^2*sr, i.e. values close to zero or complete darkness. 37.16% of all protected areas had on average lit values between 1 to 20 nW/cm^2*sr, where the maximum value was similar to brightness in the suburbs of Edinburgh. There were only six protected areas with average radiance values of 60 nW/cm^2*sr or higher: Camley Street Nature Park (99.64 nW/cm^2*sr), Trafford Ecology Park (75.17 nW/cm^2*sr), Salmon Pastures (68.84 nW/cm^2*sr), Teesmouth (80.40 nW/cm^2*sr), South Gare & Coatham Sands (90.12 nW/cm^2*sr) and South Elmsall Quarry (64.33 nW/cm^2*sr). Radiance values of

around 60 nW/cm^2*sr were found in Glasgow and Chelsea and values around 100 nW/cm^2*sr in Aberdeen, for example.

Protected landscapes were larger than most protected areas, and on average had lower radiance values (Figure 11). With the exception of Cannock Chase, all other protected landscapes showed radiance values less than 2 nW/cm^2*sr, Figure 11). The largest area, Cairngorms, had on average 0.2 nW/cm^2*sr. The Isles of Scilly, which is the smallest AONB, had on average a radiance of 0.09 nW/cm^2*sr, which is close to the threshold of darkness.

DISCUSSION

Previous studies have highlighted both the wide extent and the recent growth in artificial nighttime lighting of Britain, and elsewhere in much of Europe (e.g. Bennie et al. 2014). The data from the Suomi satellite analysed are both at a higher resolution and fully calibrated, and thus offer a more robust insight into the present situation (albeit useful information on temporal trends using this source is not yet available). They reveal that only a small proportion of the land area of Britain (here estimated at <10%) may genuinely be dark on moonless nights. Adopting a rather broader definition of near-darkness (to encompass radiance values up to 1.005 nW/cm^2*sr), this increases to c.75% of the land area. However, this still means that c.25% is measurably light-polluted. This is much greater than the area that is usually classified as urban (or suburban), reflecting the extent to which such classifications can underestimate

transport infrastructure (e.g. roads) and the marked extent of the spread of skyglow from urban centres (Biggs et al. 2012, Luginbuhl et al. 2014).

Given the spread of artificial nighttime lighting across the landscape of Britain, it is perhaps unsurprising that the ranges of a high proportion of the threatened plant species are light polluted. Indeed, the distribution ranges of only 67 of 272 species have less than 5% lit pixels (Figure 4a). Because <10% of Britain is under darkness, there is a higher likelihood that species with larger distribution ranges have a significant number of pixels being lit. In fact the five threatened species with the largest distribution ranges are at least 20% lit.

For only 26 species was 95% of the cumulative radiance contained on less than 40% of their distribution range. On the other hand, for 131 species, this 95% of the cumulative radiance was spread over more than 60% of their range. In addition to this spread, the maximum and minimum artificial light at night were very different, with many species distribution ranges having areas with very high and very low radiance values. This is a clear indication that the spread of radiance in threatened plant species in Britain is higher than that obtained for cacti species (Chapter 5) or for mammals at a global scale (Duffy et al. 2015). However, our findings in this study are at a finer spatial resolution than those obtained for cacti or for mammals, and may be an indication of the underestimation of artificial light at night at coarser resolutions, highlighting the importance of analysis at finer scales.

Although this scenario of highly spread artificial light at night in the distributions of threatened plant species in Britain might raise concerns, it is important to highlight the

percentage of ranges that have low average radiance values. Indeed, the average radiance values that CR species are receiving is 4.1 nW/cm^2*sr, much less than radiance detected in small towns or even outside these areas. This is true also for EN and VU species. The last could be encouraging if the protected areas system, which contains the occurrences of many threatened plant species (Jackson et al. 2009) was free of artificial light at night. Unfortunately, protected areas are not free of such light, with on average only 3.03% under darkness. Similar to findings in other studies (Gaston & Bennie 2015), large protected areas in Britain are better buffered against nighttime light than small areas. This might be because large areas have proportionally a larger area farther away from populated zones than smaller areas, and because protected areas are usually located in less populated sites (Jackson et al. 2008).

Artificial nighttime lighting, together with other anthropogenic disturbances, may have diverse effects on wild plant species, directly by altering individual phenology (e.g. bud burst, leaves falling down) and indirectly acting on pollinators and dispersers, by changing community composition and in turn modifying distribution ranges. Evidence from horticultural research has shown that interrupting the night period in plants with artificial light in quantities as small as 10 µmol m^{-2}s^{-1} for short periods of time (up to four hours) can cause diverse effects across species, accelerating growth and development (e.g. *Campanula sp.*, Damann & Lyons, 1996), or increasing significantly the number of leaves, leaf length, number of pseudobulbs and pseudobulb diameter (e.g. *Cymbidium aloifolium*, Kim & Kim; 2011). Recently, Park et al. (2015) showed that interrupting the night for shorter periods but with different spectral composition results in significant positive and negative effects on morphogenesis, flowering, and transcriptional factor for

different individuals of the commercial species *Dendranthema grandiflorum*. Although this is clear evidence of the effects of nighttime lighting on plants, there is a lack of studies disentangling the effects of direct lighting on natural plant species. Indeed, as highlighted by Bennie et al. (2016), there is a need for further research that combines the existing experimental physiological knowledge of the effects of the direct exposure of artificial lighting on plants, including the effects that time-exposure and spectra might cause across species, with knowledge regarding the spatial distribution of plant species and nighttime lighting.

Although further research is necessary to disentangle the effect of different radiance values on the populations of threatened plant species in Britain, the fact that the vast majority of species have some artificial nighttime lighting in their ranges indicates the high degree of erosion of their natural dark environments. In addition, the proportion of their ranges under protection has a high probability of overlapping with some radiance as well.

It is important to propose approaches to protect threatened plant species from extensive artificial nighttime lighting. While increasing the extension of protected areas might buffer them, the opportunities are limited, mainly constrained by the pressure of diverse anthropogenic activities, which are demanding more land (e.g. housing, agriculture). While not under statutory protection, protected landscapes have on average lower radiance values than protected areas, given that in general they have larger extents. Although darkness is not a common requisite for the designation of a protected landscape, there is a global initiative which considers the importance of maintaining dark environments. This initiative, the Dark Sky movement (Welch & Dick

2012, International Dark Sky Association 2015, http://darksky.org/idsp/) recognises two dark sky areas in Britain: 1) Galloway Forest Dark Sky Park, and 2) Exmoor Dark Sky Park Reserve. These areas can help to mitigate the effects of artificial light at night not only for threatened species occurring in their extents but also to all biodiversity within them.

FIGURES
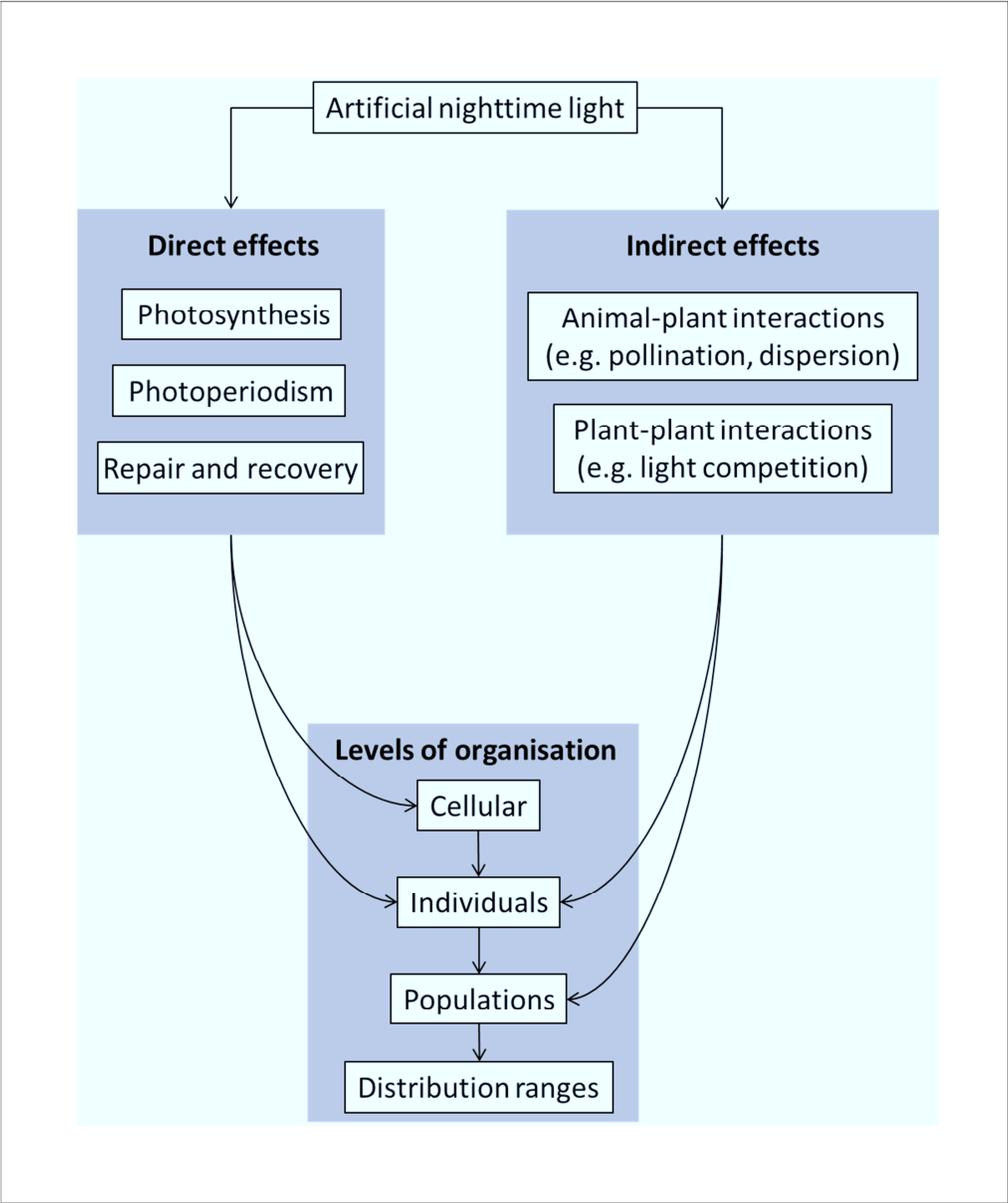
Figure 1. Effects of artificial light at night on different levels of plant organisation
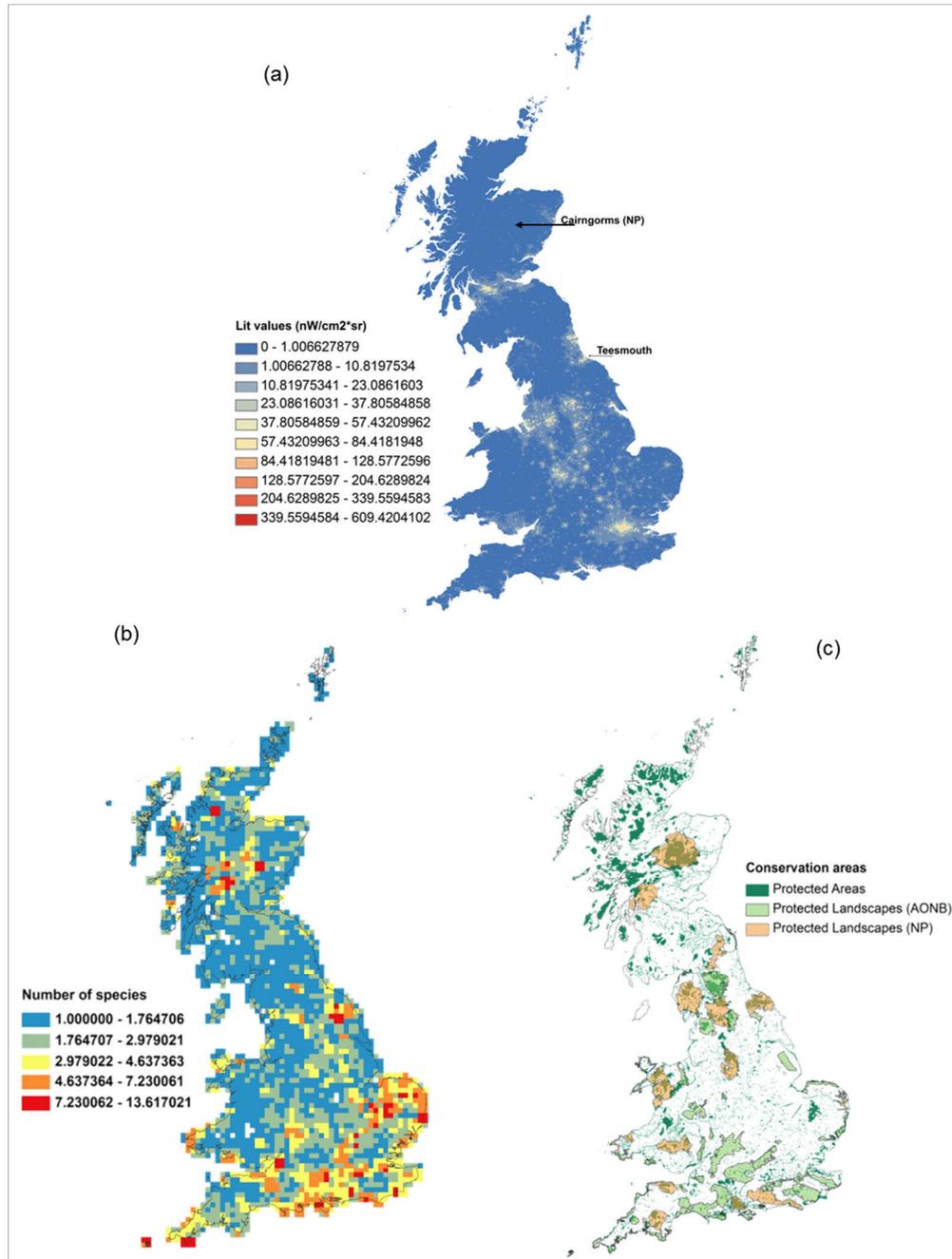
Figure 2. (a) Artificial light at night in Britain. Radiance values range from zero, representing darkness (example Cairngorms National Park) to 609.4204102 nW/cm^2*sr for the brightest area (Teesmouth, Nr Middlesbrough); (b) Distribution of 272 threatened species in Britain at 10kmx10km resolution (hectads). This resolution is used for display purposes only, data were analysed at 2kmx2km, and values presented here are averaged for all tetrads contained in an individual hectad. Jenks natural breaks were used; (c) Coverage of Protected Areas and Protected Landscapes in Britain.
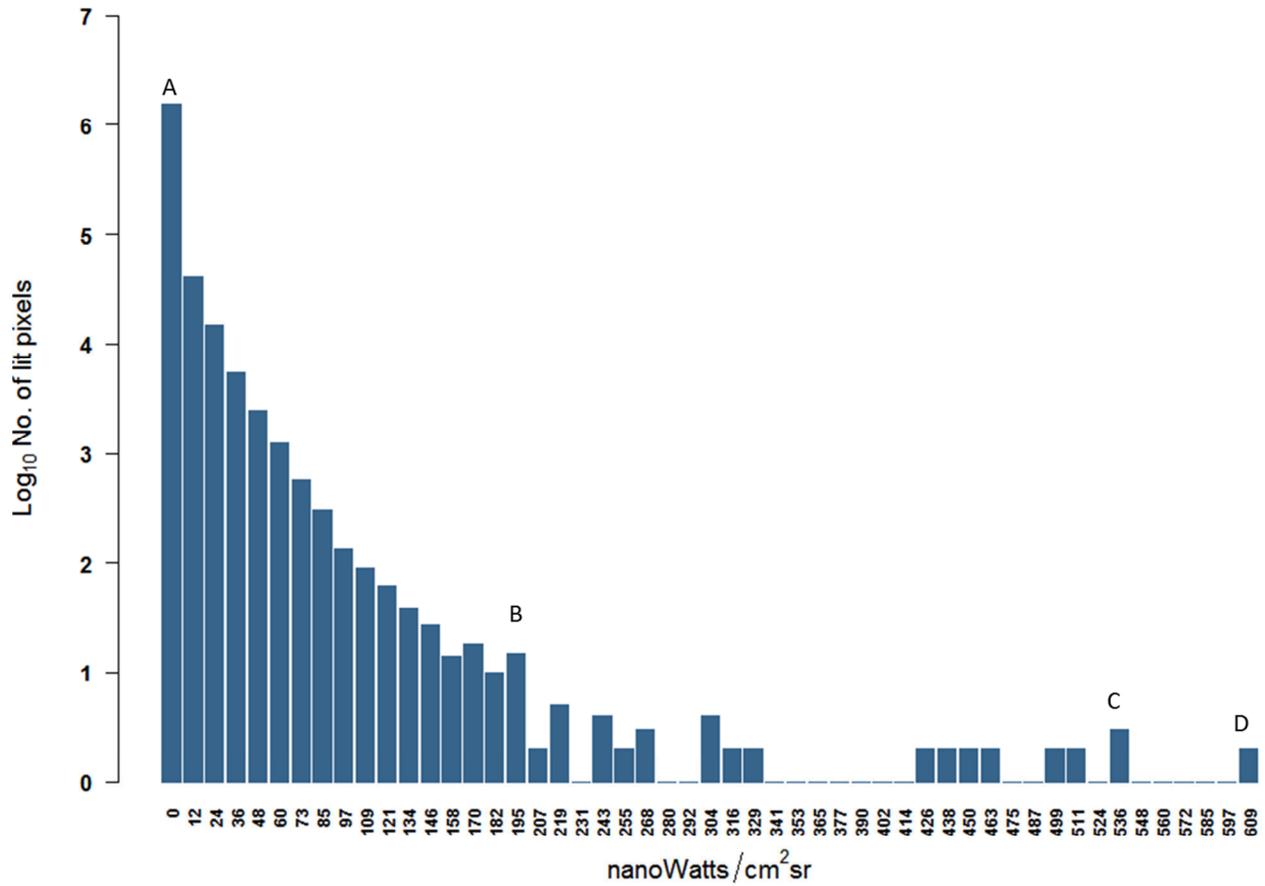
Figure 3. Frequency distribution (log. N+1) of radiance values across Britain. A) Merrick Kells and North Dartmoor, B) Manchester and London (Soho), C) Elton, Cheshire and D) Teessmouth, Nr Middlesbrough.
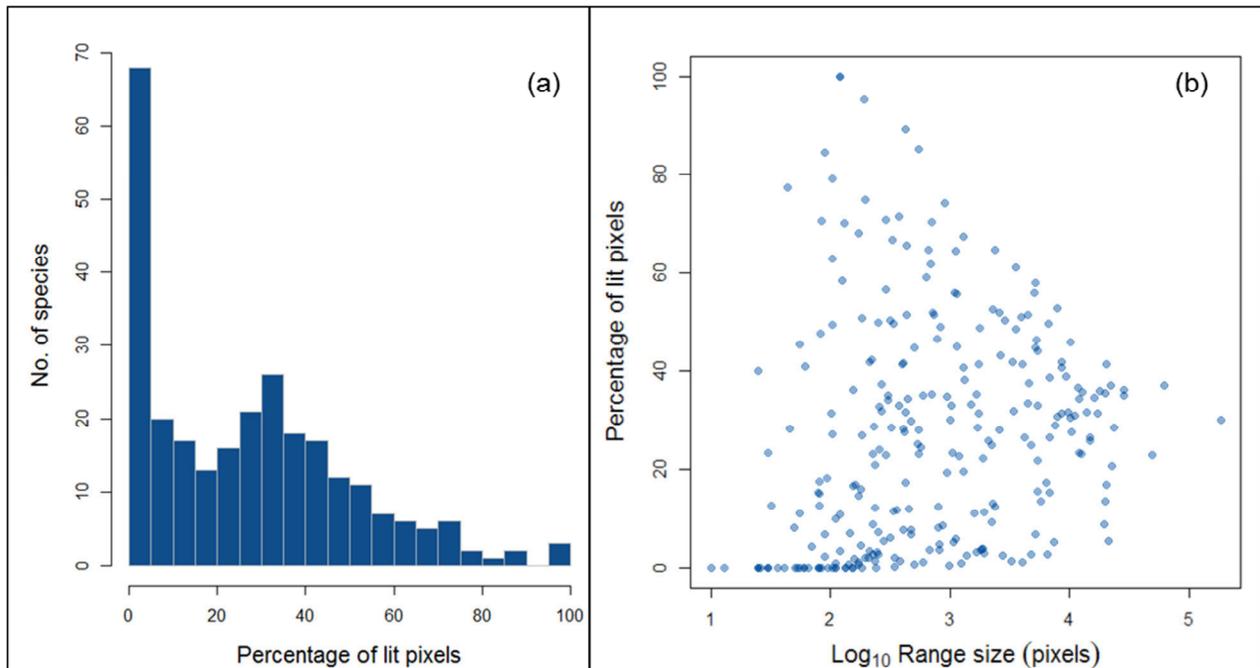
Figure 4. (a) The number of threatened plant species in Britain with different percentages of their geographic ranges lit (N=272). (b) The relationship between the percentages of the geographic range of each plant species lit and its range size. Lit pixels are considered to have radiance values >0.00001 nW/cm^2*sr.
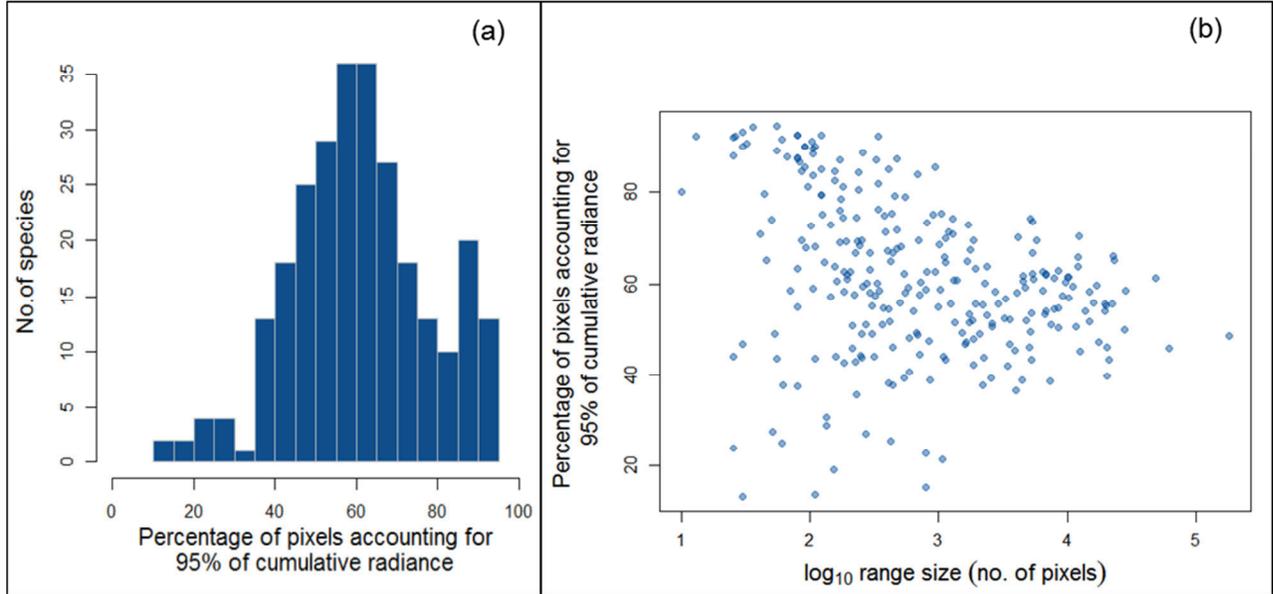
Figure 5. (a) Frequency distribution of the number of threatened plant species with a given percentage of pixels that make up the 95% cumulative radiance in their ranges. (b) The relationship between the percentage of pixels that make up the 95% cumulative radiance of each threatened plant species and its range size (number of pixels).
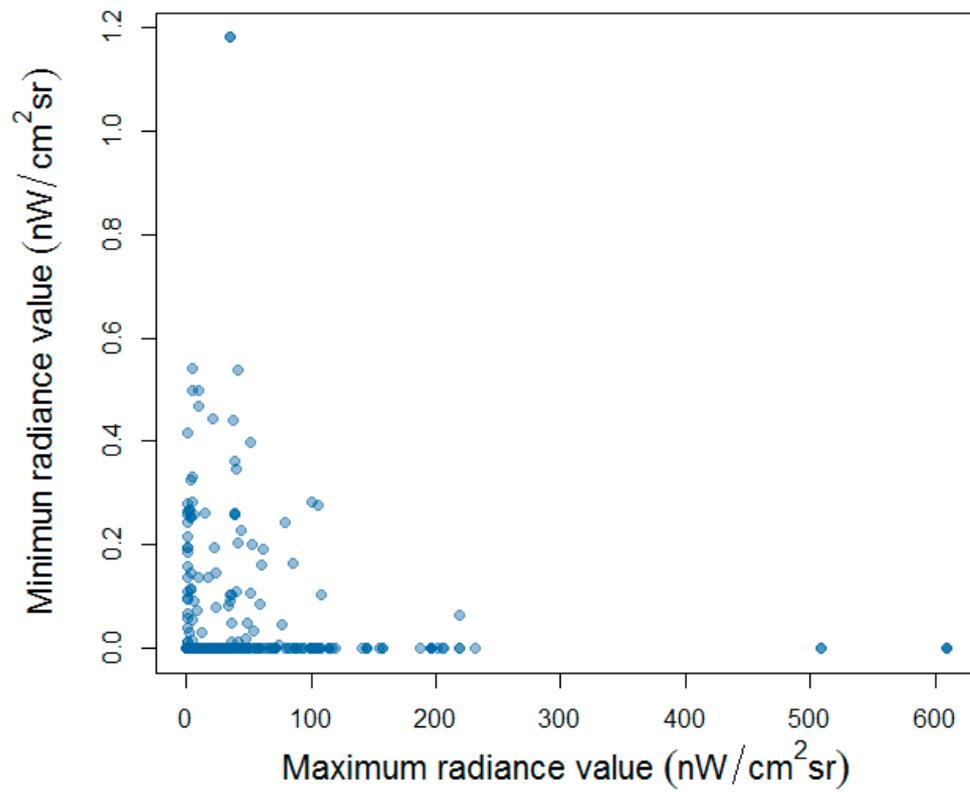
Figure 6. Relationship between the minimum and maximum radiance values in the distribution range of each threatened plant species.
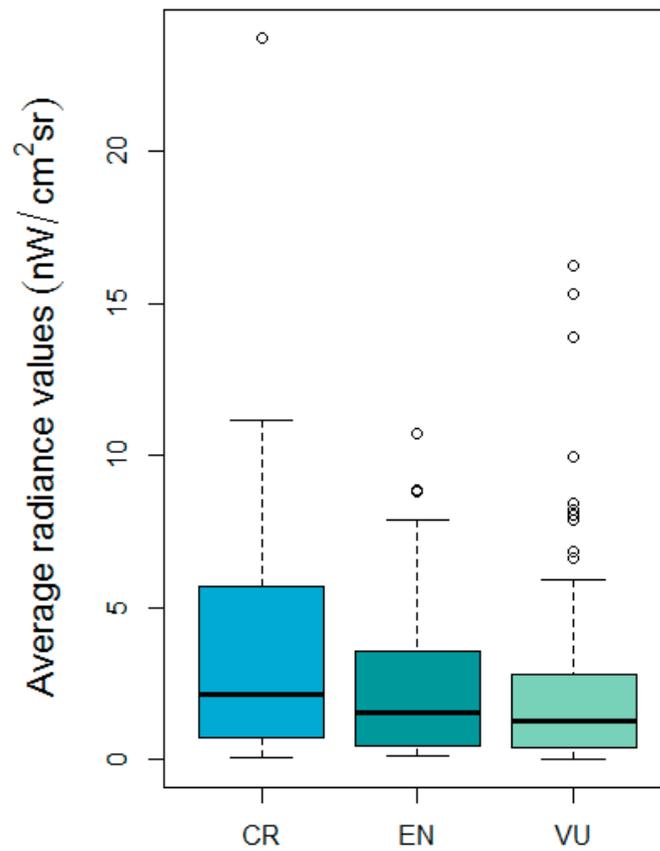
Figure 7. Averaged radiance values per IUCN categories. Critically endangered (CR, n=29), endangered (EN, n=73), and vulnerable (VU, n=170).
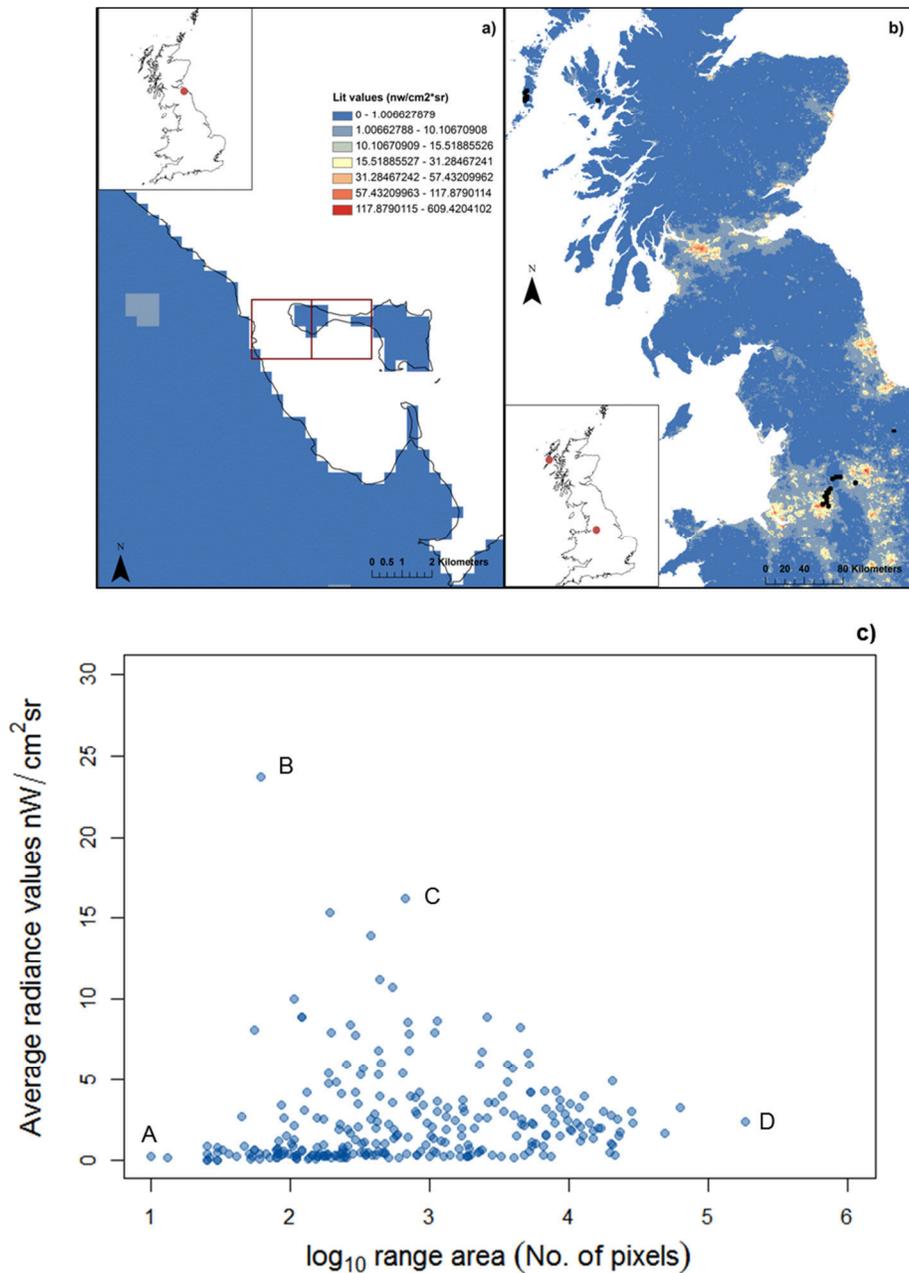
Figure 8 (a & b). Occurrence of nighttime lighting within and around the distributions of two very restricted species – (a) *Epipactis sancta* (CR), restricted to Holy Island and (b) *Potamogeton epihydrus* (VU) with a clumped distribution. Species ranges are represented with black squares. (c) Relationship between the average nighttime lighting across the distributions of each of the 272 threatened plant species and the range size of those distributions. Four species are identified for reference: A) *Epipactis sancta*, B) *Schoenoplectus triqueter*, C) *Potamogeton epihydrus,* and D) *Spergula arvensis*.
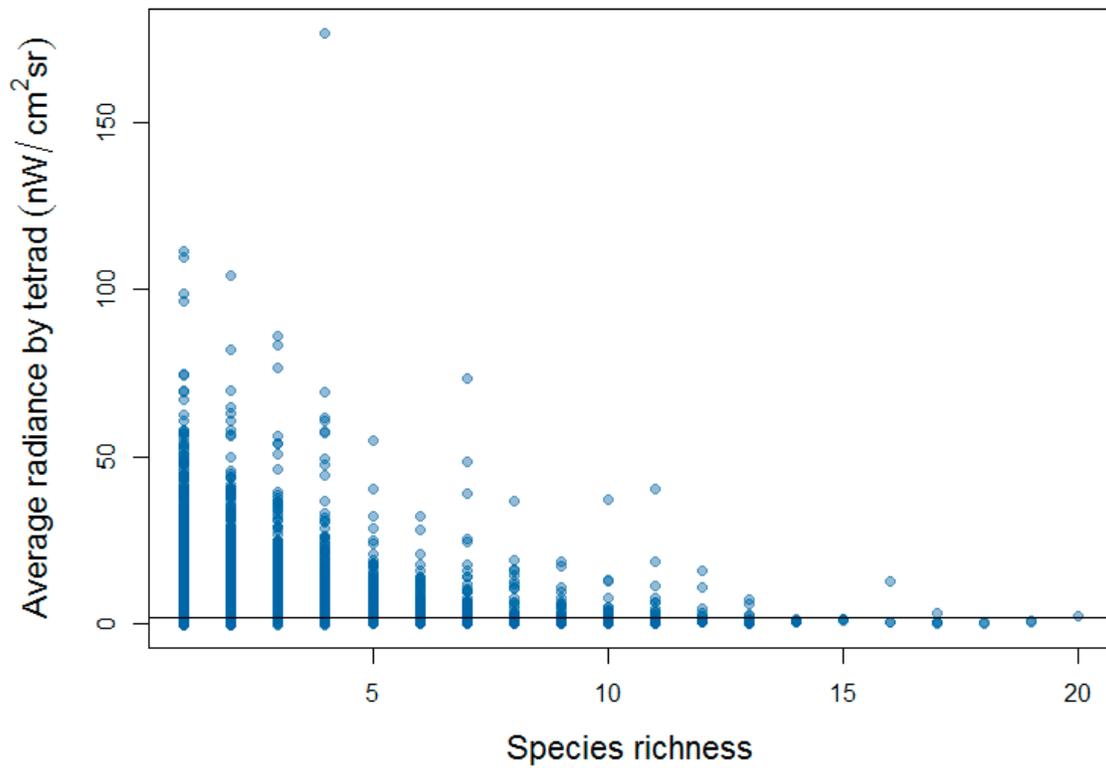
Figure 9. The relationship between the average nighttime lighting of a tetrad and the richness of threatened plant species recorded there. The tetrad with highest species richness is located at Marsworth, and the tetrad with the highest radiance value is located at Coatham Sands, North Yorkshire (radiance=176.82 nW/cm^2*sr).
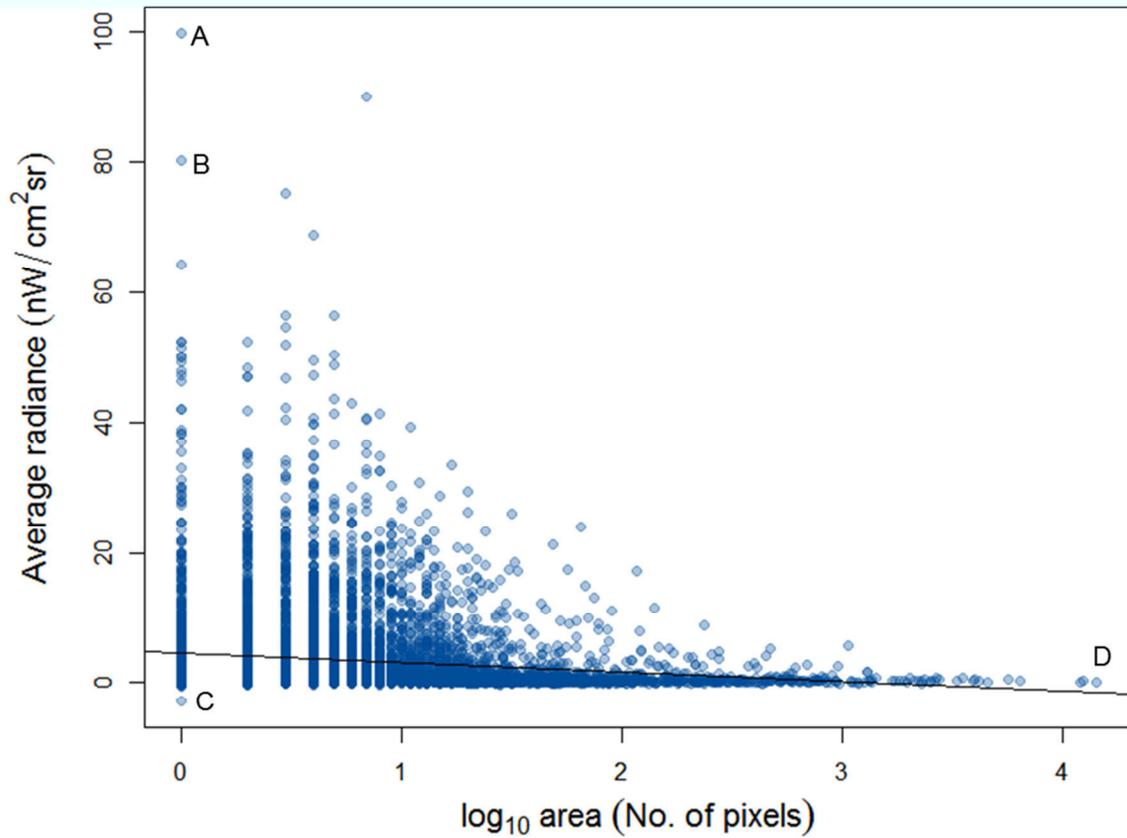
Figure 10. The relationship between the average nighttime lighting in a protected area and the extent of that protected area (number of pixels). (A) Camley Street Nature Park, (B) Teesmouth, (C) Longman and Castle Stuart Bays and (D) Caithness and Sutherland Peatlands.
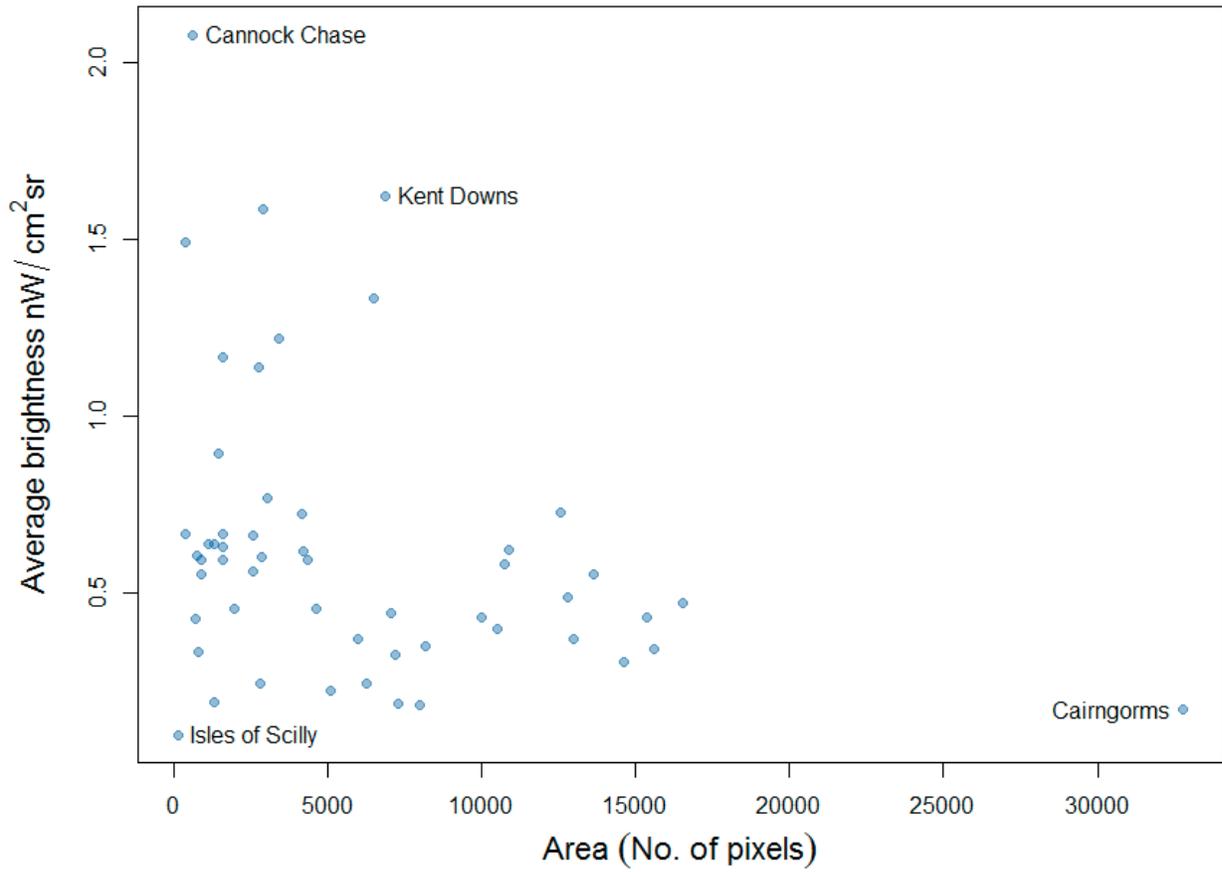
Figure 11. Relationship between the average brightness and the areas of AONBs (Areas of Outstanding Natural Beauty), and National Parks (number of pixels).

CHAPTER 7

DISCUSSION

Each analytical chapter of this thesis includes a detailed discussion of the respective results reported. In this chapter I will not repeat discussion of those same detailed topics, rather I will highlight some selected broad issues regarding the macroecology of plant species (see Chapter 1 for overview) that have emerged from the research that I have conducted.

Data availability

My original intention was that this thesis would comprise an integrated analysis of a variety of macroecological patterns for plants (e.g. individuals-area relationships, species-range size distributions, abundance-range size relationships, abundance-body size relationships). This plan relied heavily on creating a large and robust data set on the local abundances/densities of plant species. However, the development of the second and third chapters revealed a surprising paucity of such data (and resulted in a rethink in the structure of the whole thesis). First, estimates of local abundances are not widely reported in the ecological literature for plants, and thus it is not possible to collate a data set that is comparable to those that have been collected for a number of groups of animal species (e.g. Silva & Downing 1995; there were sufficient data for the analyses reported in Chapters 2 and 3, although in both cases the conclusions are qualified by limitations on what was available). Where such estimates have been

reported, even in recent papers, information is often not made available on the size of the areas from which the estimates were obtained (e.g. Steege et al. 2013, Crowther et al. 2015), greatly limiting how the data can be used (see Chapters 2 and 3); it should be standard practice that plot size information is provided alongside local abundance/density estimates for both plant and animal studies.

Second, estimates of local abundances are not collected in large survey schemes for plants in the increasingly routine fashion that they are (at least in some parts of the world) for some groups of animals (e.g. British Trust for Ornithology (BTO) schemes, The Pan-European Common Bird Monitoring scheme (PECBMS), The Breeding Bird Survey (BBS), Rothamsted Insect Surveys). An obvious exception is the data set created by Gentry (Phillips et al. 2002), but it is notable how plant macroecology has continued to be dependent on a data set produced by a single individual (rather than through a formal scheme) long after it was made available (Enquist & Niklas 2001). There are, however; two organizations that aim to gather plant data: the Global Biodiversity Information Facility (GBIF) and the Global Index of Vegetation-Plot Databases (GIVD). The GBIF is a portal from which researchers can access data bases from around the world, although the data available contain information on occurrences from floras and checklists mainly. The GIVD provides an overview of existing vegetation data collected in plots worldwide, although for 80% of the data available the size of the plots is unknown.

Not only is the availability of data an issue for plant macroecology, but so is the quality of data. The lack of availability of good quality data for the analysis of macroecological patterns for animal species, as highlighted by Gaston & Blackburn

(1999), applies to data for plant species too. Indeed, most of the data available for plants have been collected for purposes of taxonomic descriptions, generating astonishing herbarium collections across the globe, for example, in Europe the Muséum National d'Histoire Naturelle, France (>9 million specimens), Kew Botanical Gardens, UK (c.7 million specimens), in North America the New York Botanical Garden, USA (>7 million specimens), Missouri Botanical Gardens, USA (>6 million specimens), in Africa the South African National Biodiversity Institute (c.1.2 million specimens), in Asia the Chinese National Herbarium (>2 million specimens), in Australasia and Oceania the Australian National Herbarium (>1 million specimens) and in South America the Herbarium of the Universidad de Buenos Aires (c.700,000 specimens). Although invaluable, all the plant data derived from herbaria collections, monographs, or other similar sources were not collected with the purpose of being analysed at macroecological scales, typically not even with the purpose of being analysed within an ecological framework; although they have been valuable for the generation of species distribution maps

In this context one particular methodology draws my attention: the phytosociological methodology. This methodology is carried out with the aim of describing plant communities, particularly across Europe (with the exception of UK), where it has a historically long tradition (Rodwell 1995, Ewald 2001) and has generated a considerable amount of data. This methodology has been criticised for not considering objective and standardised rules during the data collection, particularly when collectors have to decide the size and position of the plots. Indeed, Chytrý & Otýpková (2003) point out that plots of diverse sizes are used to collect plant data even in a single

community type. Furthermore, evidence suggests that plot sizes are not placed at random and follow unclear criteria of when the size of plots should or should not be increased to include more species (Chytrý 2001). This has resulted in different patterns when defining the same plant communities (Ostermann 1998). In contrast to what is proposed by some authors (Schaminée et al. 2009), using data collected applying the phytosociological methodology might lead to important biases when answering macroecological questions. Bias in sampling, as considered in Chapter 2, may, for example, lead to a negative density-area relationship, a pattern that might not be caused by any biological properties, but is a likely consequence of artefacts in the sampling methodology. Conducting analyses at a determined scale with data collected at different scales can lead to observing unreliable patterns, especially because patterns in macroecology are scale-dependent (Chapter 4).

Anthropogenic activities and macroecological patterns

As mentioned in the introduction, macroecological patterns have been traditionally analysed considering that environmental and positional variables are the major drivers of the observed patterns. Recognition of anthropogenic activities as a variable which can explain an important proportion of the variation across diverse patterns is not a common approach.

Gaston (2004) proposes four probable reasons as to why macroecologists in general have not considered anthropogenic activities in analysing their models. He argues that the lack of attention may be due to 1) that the effect of human activities

might be overlooked, 2) that its effects might be considered not important in explaining variation across macroecological patterns, 3) a lack of appropriate information, and 4) that researchers may consider its effects already included when examining variables such as habitat structure or resource availability. The most likely cause of not considering human effects on macroecological patterns as an independent and greatly influential variable is probably the last one (Gaston, 2005), although a fifth reason may be that many ecologists prefer to study "natural" conditions (environmental and positional variables), hence deliberately do not consider anthropogenic activities in their models (W.E. Kunin pers. comm.). Nevertheless, there is strong evidence of the effects of anthropogenic activities on ecosystems, how deeply humans transform communities and populations of species at a global scale (Vitousek et al. 1997, Hodkinson & Thompson 1997, Noble & Dirzo, 1997, Kareiva et al. 2007), and that we should not ignore the proportion of the variation that human activities might explain of current patterns of abundance and distribution of species, body masses and other important key topics in macroecology (Chapter 3 & Chapter 4). Not in vain have Crutzen & Stoermer (2000) called the current epoch the 'Anthropocene'.

This thesis reveals how one of the most recent recognised anthropogenic pollutants, artificial light at night, is encroaching naturally dark environments of many threatened plant species at different scales. The interactive effects of this together with the already well-recognised human inflicted pressures (land degradation, land use-change, global change) are still to be disentangled, but ecologists and macroecologists should be aware of its probable effects.

Next steps

Macroecology is a branch of ecology that helps to disentangle patterns and processes at large spatial and temporal scales. The study of the macroecology of plant species adds important insights. As humans exert impact at the global scale, it is urgent to direct attention to the study of large scale patterns of plants and develop a whole program for the macroecology of plants.

Strict comparisons between patterns of animal and plant species in macroecology are not yet possible, and work on macroecological patterns for plant species has to catch-up with the understanding of patterns described for animal species. This may take considerable time and resources. Novel and different approaches are needed to complement understanding of macroecological patterns described almost entirely for animal species (e.g. abundance range-size relationships).

One option is to create a plant-macroecology program which should include:

1) Identification of relevant gaps in the study of macroecology of plant species, the patterns that have not yet been described for this realm and probable causes of their absence in the macroecological literature.

2) Directed resources to collect plant ecological data at large spatial and temporal scales, to maintain data collections, to promote their analyses and publish results. As this is a major task, a multinational effort is needed to achieve good data quality in the shortest time possible. This also means that standardisation of data collection methodologies is required, and although standardisation of field

methodologies is under constant debate, at least a random sampling and reporting of plot sizes should be an essential part of any methodology.

3) Human activities as a variable in the same rank of importance as environmental, and positional variables are considered in order to identify the main drivers of macroecological patterns.

4) Considering that for many plant species, an individual is not easily identified (e.g. for clonal species), the combination of methodologies related with coverage, remote sensing techniques and spatial analysis should be part of a holistic approach to plant-macroecology.

APPENDICES

APPENDIX 1. Introduction (Chapter 1).

Table A1. Search string used to find publications in the ISI Web of Science, based on Beck et al. 2012).

Taxon	Searching string	No. publications (Sep, 2015)
Plants: spermatophytes	macroecol* + spermatophyt* OR angiosperm* OR gymnosperm OR (plant* NOT (bryophyt* OR liverwort* OR pteridophyt* OR fern* OR alga*))	275
Plants: pteridophytes	pteridophyt* OR equiset* OR lycopodio* OR fern*	11
Plants: bryophytes	bryophyt* OR anthocero* OR marchantio* OR mosses OR liverworts	12
Plants: algae & Chromista	alga* OR diatom* OR bacillariophyta OR chlorophyta OR cyanidiophyta OR glaucophyta OR prasinophyta OR rhodophyta chromista OR cryptophyta OR haptophyta OR hyphochytriomycota OR labyrinthista OR ochrophyta OR oomycota OR sagenista	38
Animals: Chordata: mammals and birds	macroecol* + mammal* OR bird* OR avian	435
Animals: Chordata: other clases	macroecol* + reptil* OR amphib* OR fish* OR actinopterygii OR appendicularia OR ascidiacea OR cephalaspidomorphi OR cephalochordata OR elasmobranchii OR myxini OR sarcopterygii OR thaliacea	202
Animals: Arthropoda: insects	insect* OR hexapoda OR archaeognatha OR balttodea OR coleoptera OR dermaptera OR diptera OR embiidina OR ephemeroptera OR gryllblattodea OR hemiptera OR hymenoptera OR isoptera OR lepidoptera OR mantodea OR mantophasmatodea OR mecoptera OR neuroptera OR odonata OR orthoptera OR phasmida OR phthiraptera OR plecoptera OR psocoptera OR raphidioptera OR siphonaptera OR strepsiptera OR thysanoptera OR trichoptera OR zoraptera OR zygentoma OR butterfl* OR moth* OR bees OR beetles OR dragonfl* OR grasshopper*	164

Taxon	Searching string	No. publications (Sep, 2015)
Animals: Arthropoda: other clases	spiders OR crayfish OR arachn* OR branchiopoda OR cephalocarida OR chilopoda OR diplopoda OR entognatha OR malacostraca OR maxillopoda OR ostracoda OR pycnogonida OR remipedia	21
Animals: Mollusca	macroecol* + mollusc* OR aplacophora OR bivalvia OR cephalopod* OR gastropod* OR monoplacophora OR polyplacophora OR scaphopoda OR snail* OR mussel* OR cuttlefish	52
Animals: other phyla	acanthocephala OR acoelomorpha OR annelid* OR brachiopoda OR cephalorhyncha OR chaetognatha OR cnidaria OR ctenophora OR cycliophora OR echinodermata OR echiura OR ectoprocta OR entoprocta OR gastrotricha OR gnathostomulida OR hemichordata OR mesozoa OR myxozoa OR nemat* OR nemertea OR onychophora OR phoronida OR placozoa OR plathyhelminthes OR plathelminthes OR porifer* OR sipuncula OR tardigrad*	14
Total		**1224**

APPENDIX 2. Intraspecific & interspecific individuals-area relationships of plants (Chapter 2)

A2.1 Sources of plant abundance estimates analysed

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A2.2. Analysis of multicollinearity

Multiple regression analysis can be hindered by the complex nature of ecological data, in which targeted ecological responses are linked to many explanatory variables that are often correlated among each other (multicollinear; Graham, 2013).

Multicollinearity misleadingly inflates the standard errors and makes some variables statistically insignificant which would otherwise be significant. This makes multicollinearity analysis a necessity (Plexida et al. 2014).

We performed a test for multicolinearity of the bioclimatic variables (latitude, rainfall and temperature) by using the command VIF implemented in the 'car' package (John et al., 2014) in R Language and Environment for Statistical Computing.

Pair to pair comparison between covariates showed that temperature and latitude (considered as the absolute value) had the highest VIF values (5.8). The results are shown in the Table A2.2.1 below.

Table A2.2.1. Comparative VIF values obtained for the bioclimatic variables and latitude used as fixed factors on the most complex linear mixed effect model.

Variables	Latitude	Temperature	Rainfall
Latitude	1	5.8	1.7
Temperature		1	1.15
Rainfall			1

A2.3. Model selection for the interspecific individuals-area relationship

We performed linear mixed-effects models for the number of individuals and the explanatory variables (the geographic coordinate latitude and longitude, rainfall, temperature, growth form with five levels; fern, herbaceous, liana, shrub and tree; and human disturbance with two levels: disturbed and undisturbed). This analysis was applied to quantify relationships between a response variable and covariates, which can have nested covariance structure and may be unbalanced (Bolker et al 2009). We fitted the most complex model (i.e. with all additive terms and the interaction between plot area and growth form) using maximum likelihood and then followed a top-down strategy for model selection by elimination of non-significant terms using the 'step' command implemented in the 'lmerTest' library.

Elimination of the non-significant fixed effects is done one at a time following the principle of marginality: the highest order interactions are tested first; if they are significant, the lower order effects are not tested for significance (Kuznetsova et al. 2014). The automatic elimination of terms implemented by the 'step' command considers the Satterthwaite degrees of freedom calculation, since we are testing on the

boundary (Zuur et al. 2009). Population means and differences of least-squares means for the fixed part of the model are provided in table Table A2.3.1. The final model given by the elimination of non-significant terms includes plot size (logarithmic transformed), latitude, temperature and rainfall. This model was refitted with restricted maximum likelihood and the estimates are shown in Table 1 of the main text.

Table A2.3.1. Summary table of the fixed factors (significant and non-significant) after being fit by maximum likelihood with the 'lmerTest' package. Information provided is sum of squares (Sum Sq), mean squares (Mean Sq), degrees of freedom (Num DF), denominator degrees of freedom (DenDF), F.value, elimination number (elim.num) and p-values (PR(>F)).

	Sum Sq	Mean Sq	NumDF	DenDF	F.value	elim. num	Pr(>F)
Log.plotsz	31.337	31.337	1	981	69.351	0	<0.001***
Growth form	1.560	0.390	4	250	1.385	4	0.2397
Latitude	0.491	0.491	1	1108	10.014	0	0.0016 **
Longitude	0.162	0.162	1	462	2.153	2	0.143
Human.act	0.208	0.208	1	1087	0.007	1	0.9319
Temperature	0.011	0.011	1	927	6.077	0	0.0139 *
Rainfall	6.088	6.088	1	1150	28.475	0	<0.001***
Log.plotsz: growthform	1.602	0.401	4	824	1.845	3	0.1181

APPENDIX 3. Plant species richness and the historical landscape of Cornwall, UK

(Chapter 4)

Table A3.1 Summary of the HLC types analysed**.**

HLC Types	Defining attributes	HLC merged types
Upland Rough Ground	Usually with the longest human interference /utilisation. Impoverished soil supporting essentially heat/scrub vegetation communities, usually being a product of prehistoric human intervention, which was maintained through medieval and early modern land use systems.	Ancient
Coastal Rough Ground	Cornwall' cliffs that have been utilised since at least the Bronze Age. Areas which are to a considerable extent the product of thousands of years of human activity, particularly summer grazing, turf-cutting and extractive industry. Now are almost entirely neglected with very little grazing. Long distance coastal footpaths run through this type.	Ancient
Rough Ground Industrial	Mainly areas located at the coast and deeply modified since the Iron Age. Some headlands were isolated with rampart and ditches as 'cliff castles'. Sites of ancient mines and quarries.	Ancient
Dunes	Areas of blown sand and shell deposits along low-lying stretches of the Cornish shore, principally on the north cost. Human activities on these areas include summer grazing of farm animals and the deliberate introduction of marram grass, *Ammophila arenaria*, to aid stability.	Ancient
Farmland Pre-historic	Areas of agricultural heartland, with farming settlements documented before the 17th century AD, and whose field patterns are morphologically distinct from the generally straight-sided fields of later enclosure. Either prehistoric or medieval origins. Most of this type will have been enclosed and farmed since later prehistory (Middle Bronze Age onwards, from c1500 BC).	Ancient

HLC Types	Defining attributes	HLC merged types
Farmland Medieval	Same as farmland pre-historic.	Ancient
Farmland Post Medieval	Land enclosed in the 17th, 18th, and 19th centuries, usually from land that was previously upland rough ground and often medieval commons. Up to 300 years of agriculture, including, in the last 50 years, a shift from mixed to largely pastoral farming, has left evidence for several post-medieval episodes.	17th to 19th centuries
Settlement old-core (Pre-20th century)	Settled areas from larger farming settlements upwards. Farmsteads, hamlets/villages and towns that have their origins in the Early Medieval period (i.e. post-Roman and pre-Norman) which have not change their size since the Medieval Ages.	17th to 19th centuries
Ornamental	The deliberately and carefully manipulated landscape, parklands and gardens surrounding large country houses, normally of 18th and 19th century origin.	17th to 19th centuries
Ancient woodland	Comprises mainly the remnants of traditionally managed woodlands, usually found in the steep-sided valleys extending inland from creeks or coves. Many of the ancient woods have been replanted in the later twentieth century with conifers.	20th century
Plantations and Scrub	There are blocks of mainly conifers plantations. Located often beyond the crests of steep-sided valleys and creeks (the more typical locations of Cornwall's older woods). Several are on sites of more ancient woods (a type mapped by Natural England).	20th century
Farmland 20th century	Mainly anciently enclosed land or post-medieval enclosed land whose field systems have been substantially altered by large-scale hedge removal in the 20th century. It also includes 20th century intakes from rough ground, woodland and marsh. Larger fields that result from hedge removal, using heavier machinery.	20th century

HLC Types	Defining attributes	HLC merged types
Settlement 20th century	Settled areas from larger farming settlements upwards. Farmsteads, hamlets/villages and towns that have been expanded by the provision of housing estates for local families and new residences for a growing population of retired people and people wanted second or holiday homes in Cornwall. Many settlements are largely residential now, most of their original industrial, harbour and commercial functions having died, their original cores now dwarfed by 20th century expansion. Others are now dominated by the provision of facilities for tourists.	20th century
Military	Extensive modern complexes, securely fenced, including disused Second World War airfields.	20th century
Recreational	Late 19th and 20th century tourism and recreation features. Mainly golf courses, coastal chalet/caravan parks and theme parks. Smaller areas of recreational facilities are absorbed into other types, particularly 'Settlement'.	20th century
Water Reservoirs	Twentieth century water bodies retained by built dams.	20th century
Industrial working	Active areas of extractive industry (mining and quarrying).	Industrial
Industrial no-active	Non-active areas of extractive industry (mining and quarrying).	Industrial
Communications	Those main communication lines which are sufficiently large in area or significant in impact to be mapped at this scale.	No merged
Water Natural	The ground between high and low water marks on the seashore and in tidal estuaries. Inshore waters, to the 12 mile national limit are included.	No merged

APPENDIX 4. Bennie, J., Duffy, J. P., Davies, T. W., Correa-Cano, M. E., &

Gaston, K. J. (2015). Global Trends in Exposure to Light Pollution in Natural

Terrestrial Ecosystems. *Remote Sensing*, 7(3), 2715-2730.)

remote sensing

Article

Global Trends in Exposure to Light Pollution in Natural Terrestrial Ecosystems

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Abstract: The rapid growth in electric light usage across the globe has led to increasing presence of artificial light in natural and semi-natural ecosystems at night. This occurs both due to direct illumination and skyglow - scattered light in the atmosphere. There is increasing concern about the effects of artificial light on biological processes, biodiversity and the functioning of ecosystems. We combine intercalibrated Defense Meteorological Satellite Program's Operational Linescan System (DMSP/OLS) images of stable night-time lights for the period 1992 to 2012 with a remotely sensed landcover product (GLC2000) to assess recent changes in exposure to artificial light at night in 43 global ecosystem types. We find that Mediterranean-climate ecosystems have experienced the greatest increases in exposure, followed by temperate ecosystems. Boreal, Arctic and montane systems experienced the lowest increases. In tropical and subtropical regions, the greatest increases are in mangroves and subtropical needleleaf and mixed forests, and in arid regions increases are mainly in forest and agricultural areas. The global ecosystems experiencing the greatest increase in exposure to artificial light are already localized and fragmented, and often of particular conservation importance due to high levels of diversity, endemism and rarity. Night time remote sensing can play a key role in identifying the extent to which natural ecosystems are exposed to light pollution.

1. Introduction

The past century has witnessed rapid growth in the proportion of the globe that is subject to artificial light at night [1]. The development of electric lighting and the spread of both grid-based and locally generated electricity have made the widespread illumination of human settlements, roads, and industrial infrastructure possible. An unintended repercussion of this process has been the illumination of natural and semi-natural ecosystems, both through direct illumination of the environment surrounding light sources and scattered light in the atmosphere, or skyglow, which may extend the ecological effects of light pollution many tens to hundreds of kilometres beyond urban areas [2].

The intrusion of artificial light into ecosystems is of concern because there is evidence that this can have profound effects on wildlife, including plants, invertebrates, fish, amphibians, reptiles, birds and mammals [3–8], and may have effects on key ecological processes and ecosystem services [9]. Artificial light alters the natural daily, monthly and seasonal rhythms of light and dark under which species have evolved and obscures the view of the night sky that animals may use as cues for navigation; it can disrupt natural circadian rhythms, alter the activity patterns of diurnal and nocturnal animals, interfere with movement and migration in many species, and alter the timing of key events such as flowering, budburst and reproduction. However, while several studies have considered the regional changes in artificial light [10–12], it is not clearly known which types of natural ecosystem have the greatest exposure globally to the spread of artificial light.

In addition to providing a measurement of emitted light itself [1,10,13], satellite images of artificial light at night have been shown to be a proxy measure of urbanization, human population density and economic activity at national and regional scales [14–18]. From the perspective of biodiversity conservation, satellite-sensed nighttime lights represent a measure not only of the influence of artificial light, but also of other threats associated with biodiversity loss, such as habitat fragmentation and loss, industrial pollution, resource extraction and human-wildlife conflict.

The Defense Meteorological Program Operational Linescan System (DMSP/OLS), produced and distributed by the NOAA National Geophysical Data Center, provides the longest time series of publicly available data of remotely sensed nighttime lights. While higher resolution, calibrated data are available from the day-night band of the Visible Infrared Imaging Radiation Suite (VIIRS) onboard the Suomi National Polar-orbiting Partnership (Suomi NPP) satellite since 2012 [19], DMSP/OLS nighttime lights data remain highly valuable as a source for detecting longer term trends in the distribution of artificial light at night. Quantifying changes is complicated by the lack of calibration between sensors and constant (but unknown) adjustment of the gain control of the optical instrument to provide consistent imagery of cloud. Nevertheless, careful intercalibration of the data can help to standardize the images and minimize both error and bias in order to map and detect changes over time [15,20,21]. Here we use a robust regression technique, quantile regression on the median [10] to intercalibrate DMSP/OLS images and detect changes in brightness over the period 1992 to 2012 (full details given in Methods section). We combine these data with information on the global distribution of natural and semi-natural ecosystem types, derived from

high resolution (1 km) remotely sensed land cover data and the boundaries of terrestrial ecoregions (Figure 1). We use a threshold of 3 intercalibrated Digital Number (DN) units to define areas of detectable increasing or decreasing brightness. We then assess which global ecosystems have the most rapidly increasing exposure to artificial light pollution for the period 1992 to 2012.
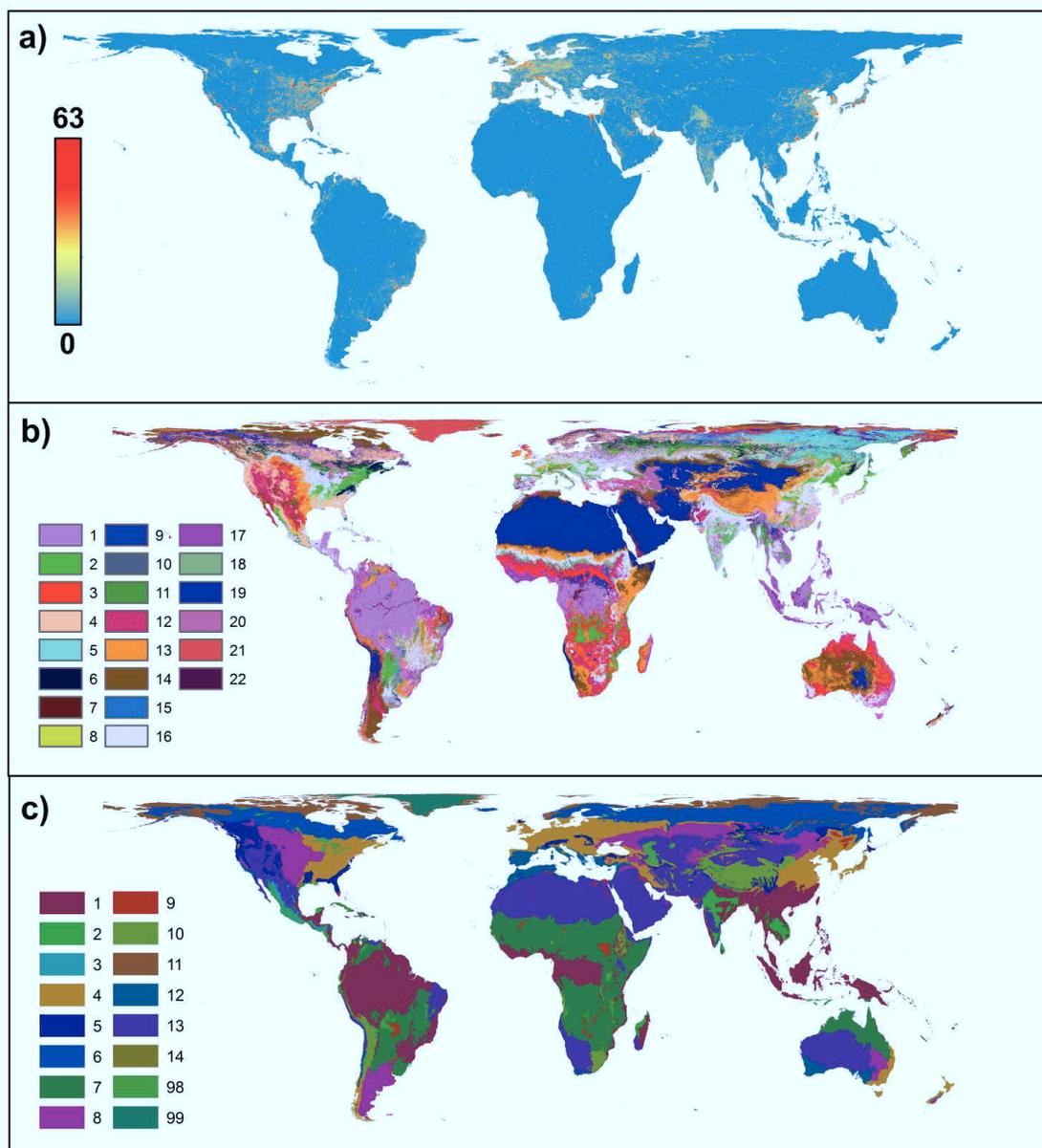
Figure 1. (**a**) Global nighttime lights image from DMSP data, 2012; (**b**) Global landcover from GLC2000, aggregated from 1 km resolution; (**c**) Global terrestrial ecoregions from World Wildlife Fund (WWF). Categories in panels b and c are coded as in Table 1.

Table 1. Classes of landcover and ecoregion used to define global ecosystem types in this study.

GLC Global Landcover Class	WWF Terrestrial Ecoregion
1. Tree Cover, broadleaved, evergreen	1. Deserts and xeric landscapes
2. Tree Cover, broadleaved, deciduous, closed	2. Tropical/subtropical moist broadleaf forests
3. Tree Cover, broadleaved, deciduous, open	3. Tropical/subtropical dry broadleaf forests
4. Tree Cover, needle-leaved, evergreen	4. Tropical/subtropical coniferous forests
5. Tree Cover, needle-leaved, deciduous	5. Temperate broadleaf and mixed forests
6. Tree Cover, mixed leaf type	6. Temperate coniferous forest
7. Tree Cover, regularly flooded, fresh water (& brackish)	7. Boreal forests/Taiga
8. Tree Cover, regularly flooded, saline water	8. Tropical/subtropical grasslands, savannas and shrublands
9. Mosaic: Tree cover/Other natural vegetation	9. Flooded grasslands and shrublands
10. Tree Cover, burnt	10. Tundra
11. Shrub Cover, closed-open, evergreen	11. Mangroves
12. Shrub Cover, closed-open, deciduous	
13. Herbaceous Cover, closed-open	
14. Sparse Herbaceous or sparse Shrub Cover	
15. Regularly flooded Shrub and/or Herbaceous Cover	
16. Cultivated and managed areas	
17. Mosaic: Cropland/Tree Cover/Other natural vegetation	
18. Mosaic: Cropland/Shrub or Grass Cover	
19. Bare Areas	
20. Water Bodies (natural & artificial)	
21. Snow and Ice (natural & artificial)	
22. Artificial surfaces	

2. Results and Discussion

All natural ecosystems considered here have experienced an increase in exposure to artificial light over this time period (Figure 2). Because areas classified in the GLC2000 dataset as "artificial surfaces" or "cultivated and managed areas" were excluded from this analysis, only a very small proportion of any ecosystem type was exposed to light at the saturation level of the sensors (the highest proportion was 0.03% at 60 DN or above, with saturation at 63 DN). We define a change in exposure of each global ecosystem type as the proportion of its area that has experienced an increase or decrease in brightness of more than 3 units (following [10]). The most marked increases are within Mediterranean ecosystems—these areas include both the Mediterranean basin itself and four other areas with a Mediterranean-type climate, typified by summer drought and a relatively mild, wet winter period, including the Cape region of South Africa, Southwest Australia, Chilean Matorral and Californian chaparral and woodlands. Mediterranean-type ecosystems harbour many "hotspots" of biodiversity and endemism, particularly for plant species—it is estimated that the Mediterranean ecoregion covers just 2% of the world's surface area but contains 20% of the world's plant species [22]. The Cape floristic region alone contains an estimated 9000 plant species, 69% of which are endemic to the region [23–25]; the South-West botanical province of Western Australia contains around 5700 plant species, 79% of which are endemic [25]. Twenty one percent of grassland and shrubland, 21% of broadleaf forest, 30% of broadleaf and needleleaf forest and 40% of mixed

forest within the Mediterranean biome have experienced detectable increases in nighttime lights. When areas which contain a mosaic of mixed natural ecosystems and agricultural land are included, 45% have experienced a detectable increase. Figure 3a,b illustrate increases in the extent of exposure to artificial light.
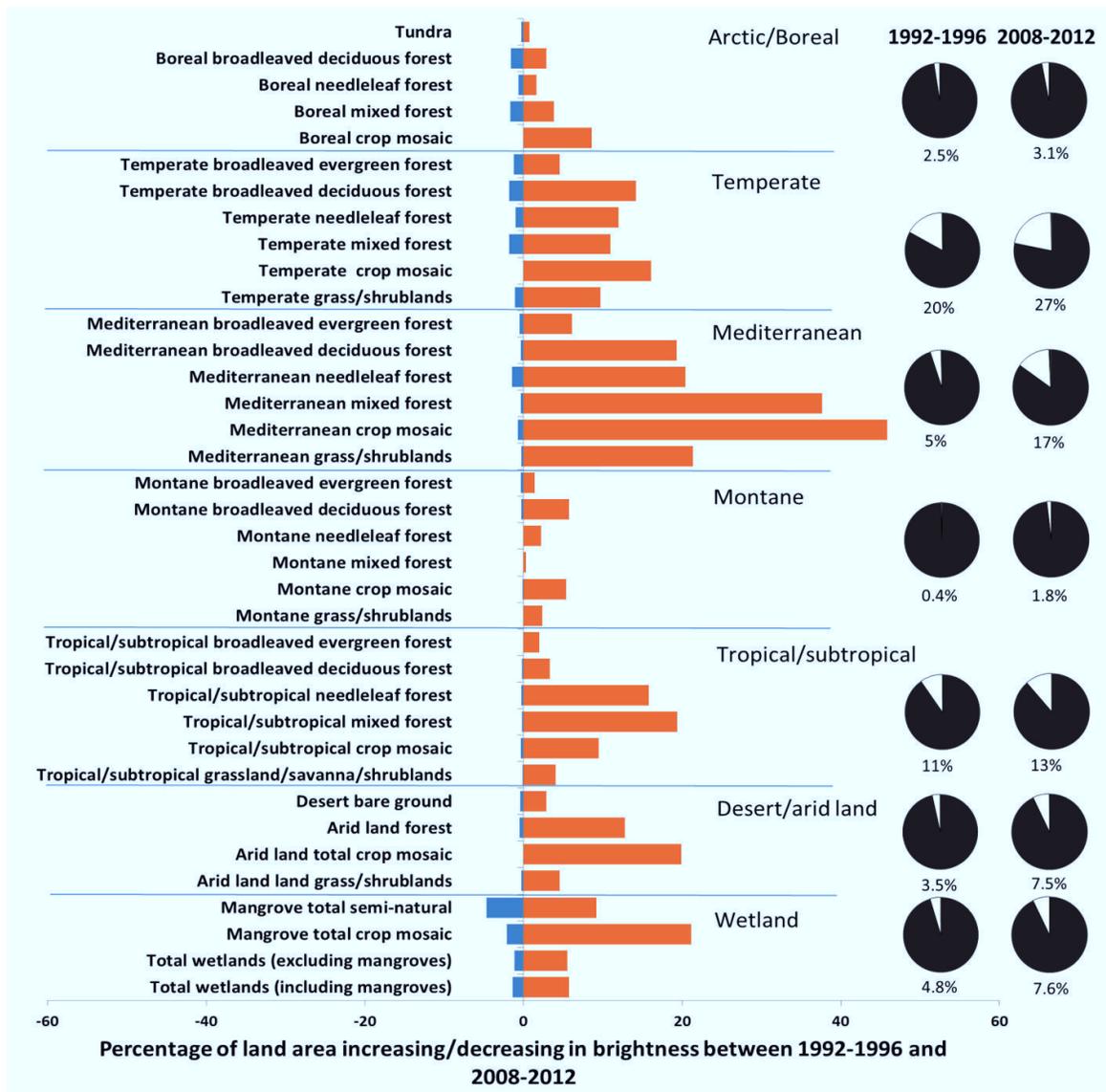
Figure 2. Horizontal bars show the percentage of total land surface area occupied by each ecosystem type for which artificial light was detected to increase (orange) and decrease (blue) by more than 3 Digital Number (DN) units between the time periods 1992–1996 and 2008–2012. Pie charts show the proportion of the natural ecosystems within each biome that had a brightness of 6 DN or greater.
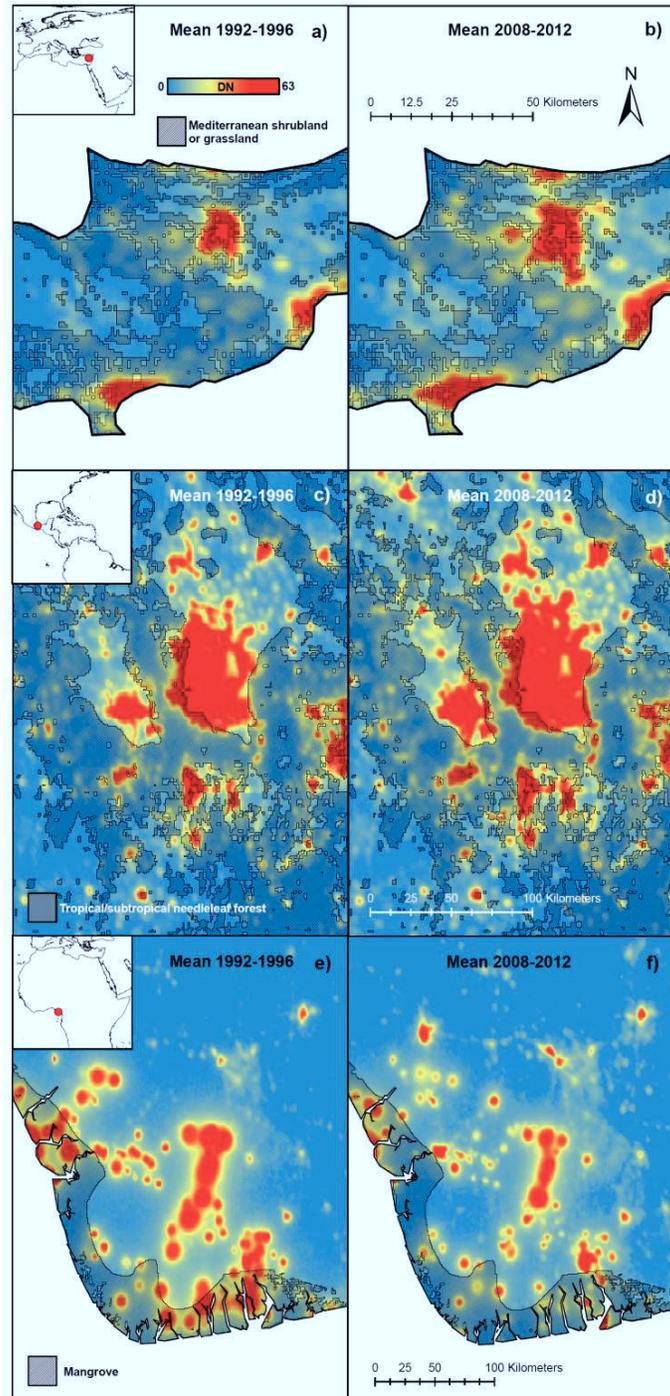
Figure 3. Selected regions illustrating encroachment of light onto natural and semi-natural ecosystems. (**a**,**b**) central Cyprus, with colour shading representing light intensity from intercalibrated DMSP/OLS data from (**a**) 1992–1997 and (**b**) 2008–2014. Cross hatched area shows the distribution of Mediterranean grassland or shrubland; (**c**,**d**) central Mexico, including Mexico City, for the same time periods. Cross hatched area shows the distribution of subtropical needleleaf and mixed forest; (**e**,**f**) the Niger Delta, Nigeria, showing the changing patterns of light emission due to changes in activity in the oil industry. Cross-hatched area shows the extent of coastal mangroves.

Temperate ecosystems have also experienced considerable increases in exposure to artificial light, ranging between 5% and 16% of the area for global ecosystem types. These regions largely coincide with rapid growth of artificial light in Europe, North America and China [1,10,15]. In the Tropical biome, the ecosystems that have experienced greatest increases in artificial light are the subtropical needleleaf and mixed broadleaf/needleleaf forests (16% and 19% respectively). Subtropical needleleaf and mixed forests are much more restricted in extent than broadleaf tropical and subtropical forests, being predominantly found in Central America, and often locally restricted to elevation bands between lowland broadleaf and high altitude cloud forest. They are characterized by high rates of biodiversity for the region; Mexican subtropical coniferous and mixed forests contain around 5300 species of flowering plants and nearly 1500 vertebrate species and contain 40% of the globally known species of trees of the genus *Pinus*, including 16 endemic species [26]. These ecosystems have experienced considerable loss in recent years; in Mexico of the 44 million hectares once occupied by the habitat, less than half (22 million ha) remains as primary forest, with a further 11 million ha as secondary regrowth [27]. In much of this region population growth and increasing urbanization have led to marked increases in light in the vicinity of these ecosystems (Figure 3c,d).

Within montane and boreal biomes, a comparatively low proportion of the land area (typically limited to less than 5% of each ecosystem type) has experienced a detectable increase in exposure to artificial light, as is also the case with deserts and arid grassland and shrubland, reflecting the low human population densities in these regions. In each case, higher rates of increase in brightness occur where semi-natural vegetation exists in a mosaic with agricultural land, and in arid biomes where patches of forest exist, often along watercourses where water is available for both vegetation growth and human settlements.

Wetlands have also experienced an increase in exposure to artificial lighting; this has been particularly marked in mangroves, which have experienced a 35% decline in global coverage since the 1970's [28]. Mangroves provide crucial ecosystem services to both the local and global community, including acting as nursery areas for commercially important fish species, providing coastal protection, detoxification of local water bodies, nutrient cycling, providing fuel and timber for local communities, supporting local biodiversity, and providing a significant source of carbon sequestration [29,30]. Nine percent of the global area of natural or semi-natural mangroves and 21% of areas of mixed mangrove and agriculture have seen an increase in exposure to artificial light. In wetlands and forested areas across all biomes there have been limited localized decreases in light intensity over the period, although these are small compared to the increases in brightness. This is often because human populations in these areas are typically smaller than those where natural vegetation exists in a mosaic with agricultural land, or where forest or wetland has been cleared or drained and converted to grassland, shrubland or aquaculture. For this reason fewer light sources are attributed to permanent settlements and roads, and more to temporary settlements and extractive industries such as forestry, fishing or mining. Figure 3e,f illustrates an example of this, showing the shifting nature of artificial light in the oilfields of the Niger Delta of Nigeria, where coastal mangroves have experienced both localised increases and decreases in artificial light over the study period.

3. Methods

3.1. Night-Time Lights Data

Twenty-one yearly (1992–2012) nighttime stable lights composite images were downloaded from NOAA [31]. These composites have been created with data from the Defense Meteorological Satellite Program's Operational Linescan System (DMSP/OLS). The images are nominally at 1 km resolution, but are resampled from data at equal angle of approximately 2.7 km resolution at the equator, and each pixel is represented by a digital number (DN) between zero and 63. A value of zero represents areas below the detection threshold, while the minimum recorded value is 3 and very brightly lit urban areas typically saturate at values of 63. For the years where two datasets were available, that from the most recently launched of the satellites was chosen. No onboard calibration of the sensors exists, and the time series includes data from several satellites with different sensors, so the brightness of images must be cross-calibrated carefully in order to assess any change in brightness. We used a robust regression technique, quantile regression through the median, that has previously been used for cross-calibration of DMSP/OLS images across Europe [10]. This method of cross-calibration is inherently insensitive to outlying values, and therefore less sensitive to changes in brightness within a calibration area, so long as the majority of pixels maintain similar light levels over time. Following [10] we first corrected for geolocation errors in the dataset by consecutively shifting each image by between −5 and 5 pixels in both the x (longitude) and y (latitude) directions and calculating the Pearson correlation coefficient of all pixels with the corresponding pixels of the image from a reference year, 2002, for which visual comparison with the land cover data suggested was accurately geolocated, matching coastlines and urban areas. The x and y offset combinations with the maximum correlation of all 121 comparisons were recorded and the coordinates of each image adjusted accordingly to maximise the match of spatial pattern between images.

Following correction for x- and y-shift, we intercalibrated images using 6th order polynomial quantile regression on the median, using the package "quantreg" [32] in the statistical software R [33]. The year 1994 was chosen as a base reference to which all other images were cross-referenced, as the image had the highest proportion of pixels with DNs of both zero and 63, by intercalibrating to this year all other images were rescaled to this range of detected values and no subsequent year's image was extended beyond the range between the minimum detectable signal and saturation. A calibration region was selected that included England and Wales, bounded by longtitude 5° W and 2° E, and latitude 50° N, 55° N. This region was selected because planning regulations in the UK have limited new urban developments over this period to a small proportion of the land area. The UK had a developed infrastructure of street lighting by the early 1990s—Unlike many other regions of Europe, there has been no widespread programme introducing new lighting infrastructure to existing settlements, even in remote and rural areas. Similarly, there have been relatively few major developments in the road network, either in terms of the widespread construction of new roads, or the widespread introduction of lighting to existing roads. Changes in lighting type over this period have also been localised. For these reasons, although the region as a whole has likely seen an increase in brightness, we consider that this increase has likely been concentrated within a minority of pixels, and hence robust regression techniques will be relatively insensitive to this increase. It is, however, impossible to test this assumption with data available for the time period of this study—although in future years VIIRS data [19] could be utilised to assess the stability and spatial

pattern of similar areas over time. An assessment of the robustness of the calibration method to increases in light intensity is given below in Section 3.4. Each consecutive year t from 1992 to 2012 was intercalibrated against this base year, by fitting the regression:

$$DN_{\text{base}} \sim c_{0,t} + c_{1,t} DN_t + c_{2,t} DN_t^2 \ldots c_{6,t} DN_t^6 \tag{1}$$

where DN_{base} is the digital number of the pixel in the base year (1994), DN_t is the digital number of the pixel in year t, and $c_{0,t} c_{1,t} \ldots c_{6,t}$ are a set of six fitted regression constants used in converting raw digital numbers to a number intercalibrated against the base year.

3.2. Land Cover Data

The World Wildlife Fund's terrestrial "Ecoregions of the World" shapefile [34] was used to define broad biome types. The data are a biogeographic regionalization of Earth's terrestrial biodiversity and contains 867 ecoregions split into 14 different biomes [35].

The Global Land Cover (GLC) 2000 [36] product was used to determine land cover within the broad biome types. This project harmonises various regional windows standardised with 22 landcover types. It has been produced at a 1 km resolution and is derived from the VEGA 2000 dataset: a dataset of 14 months of pre-processed daily global data acquired by the VEGETATION instrument on board the SPOT 4 satellite.

The biome and land cover types were combined to define 43 ecosystem types (Table 2).

3.3. Processing

All data were re-projected to the Behrmann equal-area projection, and the WWF ecoregion data were split eight broad biome categories: (a) Boreal/Tundra; (b) Desert/Shrubland; (c) Flooded; (d) Mangroves; (e) Mediterranean; (f) Montane; (g) Temperate; (h) Tropical/subtropical, using ArcMap 10 (ESRI, 2011). The following was performed using the statistical package R [33] with the packages "rgdal" [37] and "raster" [38]. An average calibrated image for both the first (1992–1996) and last (2008–2012) five years was created. Then, each of the 22 landcover classes from the GLC data was in turn subset (*i.e.*, one raster created for each class) and used as a mask on both of the average light images, resulting in two images of nighttime lights per landcover class. The nine previously mentioned biome groups were then used as masks to split further the 22 images for both the start and the end of the time series. This resulted in 396 images in total.

The biome data and landcover type were combined according to Table 1, to provide high-resolution information about ecosystem type. Pixels were classified according to the most likely ecosystem. For example, pixels within the Boreal or Arctic biome that have predominantly herbaceous or shrub vegetation were interpreted as representing tundra. Pixels for which the landcover was classified as artificial surfaces, water bodies or snow and ice were not considered in this analysis, however, where pixels were classified as mosaics of cropland and natural or semi-natural vegetation, these were analysed separately. Due to the masking of artificial surfaces, urban areas were not considered in the analysis. We did not allow for changes in ecosystem type over the period.

Table 2. Classification of ecosystem type from World Wildlife Fund (WWF) biome and Global Land Cover 2000 (GLC2000) land cover type. Columns represent WWF biomes and rows represent GLC2000 land cover within the biome; text within the table represents ecosystem type used in this study. Abbreviations: Med. = Mediterranean, Mon. = Montane, Temp. = Temperate, T/S = Tropical/subtropical. NA = not classified.

Land Cover		Biome (WWF)							
GLC Code	Land Cover Classification (GLC2000)	Boreal/Arctic (7,12)	Mangrove (14)	Mediterranean (13)	Montane (11)	Temperate (5,6,9)	Tropical/subtropical (2,3,4,8)	Desert (1)	Flooded (10)
1	Tree cover broadleaved evergreen	NA	Mangrove	Med. broadleaf evergreen forest	Mon. broadleaf evergreen forest	Temp. broadleaf evergreen forest	T/S broadleaf evergreen forest	Arid forest	Other wetland
2	Tree cover broadleaved deciduous closed	Boreal broadleaf forest	Mangrove	Med. broadleaf deciduous forest	Mon. broadleaf deciduous forest	Temp. broadleaf deciduous forest	T/S broadleaf deciduous forest	Arid forest	Other wetland
3	Tree cover broadleaved deciduous open	Boreal broadleaf forest	Mangrove	Med. broadleaf deciduous forest	Mon. broadleaf deciduous forest	Temp. broadleaf deciduous forest	T/S broadleaf deciduous forest	Arid forest	Other wetland
4	Tree cover needle-leaf evergreen	Boreal needleleaf forest	NA	Med. needleleaf forest	Mon. needleleaf forest	Temp. needleleaf forest	T/S needleleaf forest	Arid forest	Other wetland
5	Tree cover needle-leaved deciduous	Boreal needleleaf forest	NA	Med. needleleaf forest	Mon. needleleaf forest	Temp. needleleaf forest	T/S needleleaf forest	Arid forest	Other wetland
6	Tree cover mixed leaf type	Boreal mixed forest	Mangrove	Med. mixed forest	Mon. mixed forest	Temp. mixed forest	T/S mixed forest	Arid forest	Other wetland
7	Tree cover regularly flooded, fresh water	Boreal/Arctic wetland	Mangrove	Med. wetland	Mon. wetland	Temp. wetland	T/S wetland	Aridland wetland	Other wetland
8	Tree cover regularly flooded, saline water	Boreal/Arctic wetland	Mangrove	Med. wetland	Mon. wetland	Temp. wetland	T/S wetland	Aridland wetland	Other wetland
9	Mosaic: tree cover/other natural vegetation	Tundra	NA	Med. shrub/grassland	Mon. shrub/grassland	Temp. shrub/grassland	T/S shrub/grassland/savanna	Arid shrub/grassland	Other wetland
10	Tree cover, burnt	NA	NA	NA	NA	NA	NA	NA	Other wetland
11	Shrub cover, closed-open, evergreen	Tundra	Mangrove	Med. shrub/grassland	Mon. shrub/grassland	Temp. shrub/grassland	T/S shrub/grassland/savanna	Arid shrub/grassland	Other wetland

Table 2. *Cont.*

GLC Code	Land Cover Classification (GLC2000)	Boreal/Arctic (7,12)	Mangrove (14)	Mediterranean (13)	Montane (11)	Temperate (5,6,9)	Tropical/subtropical (2,3,4,8)	Desert (1)	Flooded (10)
12	Shrub cover, closed-open, deciduous	Tundra	Mangrove	Med. shrub/grassland	Mon. shrub/grassland	Temp. shrub/grassland	T/S shrub/grassland/savanna	Arid shrub/grassland	Other wetland
13	Herbaceous cover, closed-open	Tundra	NA	Med. shrub/grassland	Mon. shrub/grassland	Temp. shrub/grassland	T/S shrub/grassland/savanna	Arid shrub/grassland	Other wetland
14	Sparse herbaceous or sparse shrub cover	Tundra	NA	Med. shrub/grassland	Mon. shrub/grassland	Temp. shrub/grassland	T/S shrub/grassland/savanna	Desert/semidesert	Other wetland
15	Regularly flooded shrub and/or herbaceous cover	Boreal/Arctic wetland	Mangrove	Mediterranean wetland	Montane wetland	Temp. wetland	T/S shrub/grassland/savanna	Aridland wetland	Other wetland
16	cultivated and managed areas	NA	NA	NA	NA	NA	NA	NA	NA
17	Mosaic: cropland/treecover/other natural vegetation	Boreal crop mosaic	Mangrove crop mosaic	Med. crop mosaic	Mod. crop mosaic	Temp. crop mosaic	T/S crop mosaic	Arid crop mosaic	Other wetland
18	Mosaic: cropland/shrub or grass cover	Boreal crop mosaic	Mangrove crop mosaic	Med. crop mosaic	Med. crop mosaic	Temp. crop mosaic	T/S crop mosaic	Arid crop mosaic	Other wetland
19	Bare areas	NA	NA	NA	Montane desert/semidesert	NA	NA	Desert/semidesert	Other wetland
20	Water bodies	NA	NA	NA	NA	NA	NA	NA	NA
21	Snow and ice	NA	NA	NA	NA	NA	NA	NA	NA
22	Artificial surfaces	NA	NA	NA	NA	NA	NA	NA	NA

3.4. Assessment of Error and Bias

In order to assess the level of error and bias expected within 5-year averaged cross-calibrated DMSP images, we compared cross-calibrated images derived from different satellites but for the same year, for the time period 1997 to 2001, which was not used during this study. During this period data independently derived from at least two satellites were available—DMSP-F12 and DMSP-F14 (1997 to 1999) and DMSP-F14 and DMSP-F15 (2000 to 2006). Root Mean Squared Error (RMSE), a measure of the "noise" in the dataset, and Mean Error (ME), a measure of systematic bias, were obtained for 5-year averages from 1997 to 2001 obtained from using independent sets of both the cross-calibrated data and raw, uncalibrated data. A sample of 1 million pixels was obtained from each image to calculate error statistics; pixels which had no detectable light in any image (DN = 0) were omitted to prevent the consistent detection of continuous darkness (for example in oceans) from influencing the error statistics. The uncalibrated data had a ME of 1.25 DN, while in the calibrated data this was reduced to 0.35 DN. The RMSE of both uncalibrated and calibrated data sets was similar (4.68 and 4.61 respectively). If only the areas covered by the (semi-)natural ecosystems used in this study were included (*i.e.*, omitting urban and cultivated regions in addition to consistently dark pixels), the ME was 0.32, and the RMSE was further reduced to 2.04. Using this dataset, 95.5% of all pixels were within 3 DN and 97.9% were within 4 DN following intercalibration.

To assess the effect of increases in light in the calibration region over time on the intercalibrated values, we performed two calibrations on the data for 1994 from the DMSP-F10 satellite (using the values for the same year from the DMSP-F12 satellite as a reference). In the first calibration, the calibration coefficients were calculated in the normal way. In the second, prior to calibration 50% of pixels in the DMSP-F10 image were selected and their value was increased by 50% (truncated to a maximum value of 63). The aim was to simulate a situation where a high proportion of the calibration area underwent a considerable increase in brightness. Both sets of calibration coefficients were then applied to the original DMSP-F10 image separately. A sample of 1 million pixels from was obtained from each image to calculate error statistics, omitting continuously dark, urban and cultivated pixels as above. The ME between these images was −0.66, indicating that under these conditions the images would slightly underestimate the brightness of pixels at later dates; the RMSE was 1.55. A total of 92.3% of the pixels had values within 3 DN and 97.6% within 4 DN. We consider that the quantile regression is robust to large directional changes in brightness over a high proportion of the area of the calibration region. Bias due to excessive increases in brightness within the calibration region would lead to dimmer global estimates in later years, so any observed increases in brightness are likely to be a conservative estimate of the true values.

3.5. Change Detection

Only those pixels increasing or decreasing more than a threshold of three intercalibrated DN units were considered as a change in exposure to artificial light. This threshold was found in a previous study to minimise the number of pixel clusters in which change was detected that could not be attributed to known changes in light intensity on the ground [10]. Given the low level of bias within the cross-calibrated datasets, it is unlikely that a consistent directional trend within an ecosystem type would be detected by chance using this threshold. To test the sensitivity of our results to the choice of threshold, particularly

for dark pixels which could change from 0 to 3 DN under a relatively small increase in brightness, we repeated the analysis using a higher threshold of 4 DN, and compared the proportion of the area under each ecosystem type that increased or decreased above each threshold. Using a threshold of 4 DN decreased the area of detected change (by an average of 18% for increases in brightness and 24% for decreases), but the proportion of each ecosystem type that changed was highly correlated ($R^2 = 0.991$ for increases, $R^2 = 0.973$ for decreases). We conclude that the qualitative results of this study are insensitive to a choice of a higher detection threshold for changes in brightness.

4. Conclusions

We show that all global terrestrial ecosystem types experience some degree of exposure to artificial light, and that this exposure is increasing. Those global ecosystems experiencing the most widespread increases in artificial light are already localized and fragmented [39], and may be of particular conservation importance due to high diversity, high levels of endemism and rarity. They are often at risk from a range of other pressures associated with urban encroachment, habitat loss and fragmentation, resource extraction and disturbance [28,40]. Mediterranean and temperate ecosystems, subtropical needleaf and mixed forest, and mangroves are particularly exposed to increasing levels of artificial light, as are forests in arid zones and natural vegetation wherever it occurs in close proximity to agricultural land. More natural ecosystems are likely to experience temporally dynamic patterns of light, perhaps associated with extractive industries rather than permanent settlements.

While DMSP/OLS provides the longest time series of global nighttime lights satellite data, and are currently unique in their ability to track changes in light pollution over time, VIIRS provides opportunities for monitoring light pollution at a higher spatial resolution; other sources of remotely sensed data such as photographs from the International Space Station [41] may also prove useful. However, remotely sensed upwelling light is only a proxy for biologically significant light at ground level, and trends must be treated with caution for several reasons. Firstly, the spectral response of the OLS instrument differs from that of human or animal vision, or the action spectra of biological processes. Secondly, remotely sensed upwelling light may not be strongly correlated with direct illumination of the environment and the horizontal emissions that cause the most skyglow. Finally, the spatial resolution and accuracy of DMSP/OLS imagery causes urban lights to be detected as somewhat blurred shapes—it is not clear to what extent the area over which light is detected corresponds to the area at which biologically significant light is detectable at ground level. Indeed, there is a need for both models to approximate the intensity of light detected by organisms at the surface from satellite images [1] and for an improved understanding of the intensity thresholds for biological impacts [6]. Any assessment of exposure to artificial light should ideally be complemented by an assessment of the sensitivity and resilience of different ecosystems to light pollution. Some groups of species, such as nocturnal invertebrates and bats [42–44], are known to be particularly sensitive to artificial light at night. However, the effects on populations of animals and plants, and effects at the level of the ecosystem, are poorly understood [8]. As our understanding of the ecological effects of light pollution grows, we need to combine this knowledge with careful monitoring of the extent to which light pollution is encroaching into our natural environment.

Acknowledgments

Author Contributions

Jonathan Bennie, James P. Duffy and Kevin J. Gaston conceived the study. Jonathan Bennie and James P. Duffy carried out the analysis. Jonathan Bennie wrote the first manuscript draft and all authors contributed to revisions.

Conflicts of Interest

The authors declare no conflict of interest.

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