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A mesma pressão, diferentes reações: Serviços ecossistêmicos realizados por morcegos sob risco no Brasil

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Aos que virão

AGRADECIMENTOS

ÍNDICE

APRESENTAÇÃO

A apresentação abaixo introduz o escopo teórico e conceitual da pesquisa resultante do mestrado: "Same pressure, diferente reactions: Ecosystem Services by Bats at Risk in Brazil". Uma breve descrição de seus métodos, dos resultados obtidos e das principais conclusões também será apresentada. O texto original foi escrito em formato de artigo e submetido à revista PlosONE.

A diversidade de espécies é uma das forças que movem o funcionamento dos ecossistemas. O papel funcional da diversidade vem sendo discutido pela comunidade acadêmica como um necessário foco para biologia da conservação há décadas (Walker, 1992). A mudança do paradigma taxonômico para o funcional foi introduzida pela notória necessidade de implementação de novas estratégias de defesa dos sistemas ambientais frente às taxas de perda de biodiversidade. Com isso, "Como a diversidade biológica se relaciona com função ecológica" se tornou uma pergunta central em ecologia, impulsionando estudos que culminaram no desenvolvimento de diversos modelos teóricos que buscavam explicar as possíveis relações entre diversidade e função (Ver Peterson et al. 1998).

A mudança de uma abordagem taxonômica para uma abordagem funcional traz a tona outros aspectos da biodiversidade que antes eram obscurecidos com tradicional foco nas espécies *per se*. A perda de espécies passa a ter um outro significado pois, a depender do contexto e magnitude, extirpações de espécies podem se refletidas em mudanças em processos ecossistêmicos como produtividade primaria e decomposição (Hooper et al. 2012). Essencialmente, função ecossistêmica muda não somente devido à perda de espécies, mas devido à associada perda da função ecológica (i.e. interações interespecíficas) estabelecida por suas populações (Valiente-Bauneat et al., 2015). De forma semelhante, através de perturbações incessantes,

populações podem persistir em abundâncias tão baixas que perdem qualquer influência sobre os ecossistemas, situação conhecida como extinções funcionais ou ecológicas (Redford, 1992; Janzen, 2001).

Um dos desafios de trabalhar com diversidade funcional é que não existem fronteiras óbvias ou objetivas para a classificação de espécies em grupos funcionais (Simberloff & Dayan 1991). Umas das maneira propostas para se classificar a biota em termos de processos é a aplicação do conceito de guilda (Walker, 1992). Guilda se refere a um grupo de espécies que exploram uma mesma classe de recursos ambientais e de forma semelhante (Root, 1967). A ideia por trás do uso desse conceito é de que espécies pertencentes a mesma guilda possuem papéis ecológicos semelhantes e podem ser tratadas enquanto uma unidade funcional (Gitey & Noble, 1997).

Dentro de uma mesma guilda espécies podem ter papéis mais centrais ou mais periféricos na função associada. Por exemplo, carnívoros terrestres formam um grupo funcional de 245 espécies as quais se reúnem enquanto guilda pela dependência comum do recurso animal. A carnivoria age no controle de populações e possui efeitos que vão do topo à base da cadeia trófica, sendo um grupo essencial na regulação de comunidades e ecossistemas (Ripple et al. 2014). No entanto, há significativa diversidade de tamanho corporal entre eles, e estudos que testaram o efeito da remoção de carnívoros nos ecossistemas indicam uma relação entre tamanho e influência ecológica, com espécies maiores sendo mais importantes (Borer et al. 2005; Ripple et al. 2014). Essa relação entre tamanho corporal e influência ecológica pode ser observada em outros grupos e surge devido a um conjunto de características da história de vida dos organismos estar correlacionadas com tamanho (Peter 1998, Brown et al. 2004).

O estudo dos efeitos da diversidade funcional sobre o funcionamento dos ecossistemas tem crescido, com cada vez mais evidências apontando a importância da conservação de espécies para a manutenção de ecossistemas funcionais e resilientes (Lefcheck et al. 2015). A abordagem ganha centralidade com o crescimento da pauta de serviços ecossistêmicos (Armstrong et al. 2012), definidos como todos os benefícios, diretos e indiretos, que as pessoas obtêm dos ecossistemas. Um marco para a consolidação dessa abordagem foi a publicação do Millennium Ecosystem Assessment (MEA, 2005). Nele, reconhece-se a dependência do bem-estar humano aos serviços prestados pela natureza, incluindo todos os processos que mantêm os ecossistemas (e.g. ciclagem de nutrientes, formação de solo, produtividade primária), que em seu funcionamento promovem serviços diversos.

Se esses serviços são derivados do funcionamento dos ecossistemas e a diversidade possui um papel central na regulação desse funcionamento, pode-se considerar então, populações, comunidades e grupos funcionais como provedores de serviços ecossistêmicos (*Ecosystem services providers* ou ESP, Ver Kremen, 2005). Entre esses serviços estão o de polinização, supressão de pragas e dispersão de sementes (Howe, 1982; Fleming and Sosa 1994; Maine and Boyle, 2015). Da mesma forma que tamanho está relacionado à influência ecológica, ele também estará relacionado com provisão de um serviço, pois se correlaciona a uma gama de caracteres que proporcionam ao provedor do serviço maior efetividade na sua entrega ou maior importância funcional (Balvenera et al. 2005). Essa relação é observada em serviços ligados à redes mutualísticas (e.g. polinização e dispersão de sementes), com evidências sugerindo que tamanho corporal age como determinante do número e da força das ligações (Woodward et al 2005). Nessas redes é comum que a distribuição

de tamanhos corporais seja enviesada para espécies menores, tornando o papel funcional de espécies maiores menos redundante (Zamora, 2000).

Assume-se então o pressuposto de que tamanho do corpo é um atributo de efeito (*effect trait*, Ver Luck et al. 2012). Isto é, que o tamanho de um organismo está relacionado á sua eficiência funcional (Kremen, 2005). Por exemplo, peixes maiores da espécie *Piracatus mesopotanicus* foram observados carregando mais sementes intactas no seu intestino do que peixes menores (Galetti et al 2008). Isso torna peixes maiores dispersores de sementes mais eficientes do que peixes menores. Essa relação também é defendida pelos serviços prestados por aves. Tamanho corporal em aves está relacionado à taxa metabólica, comportamento de forrageio, longevidade, tamanho de território e com a capacidade de atravessar manchas de habitats distintos (Luck et al. 2012). Em conjunto, esses aspectos influenciariam a contribuição de polinização e dispersão de sementes por aves (e.g. volume de néctar removido, área de polinização, volume de polén transferido por visita, tamanho e número de sementes dispersadas, conectividade entre áreas, etc). Preocupantemente, tamanho corporal também está correlacionado à suscetibilidade a distúrbios de habitat e a extinção (Cardillo et al. 2008; Dirzo et al. 2014).

É nesse contexto teórico que o trabalho se insere, escolhendo a fauna de morcegos do Brasil como objeto de estudo. Em termos de diversidade, taxonômica e funcional, morcegos possuem papel destaque. Formam a segunda maior ordem de mamíferos, contabilizando 1386 espécies globalmente (Burgin et al., 2018) e 182 espécies somente no Brasil (Nogueira et al., 2018). Por meio de adaptações morfológicas e sensoriais, morcegos exploram uma grande variedade de recursos e habitats (Dumont et al., 2011), encontrando alimento em frutos, insetos, néctar, pólen, pequenos vertebrados e até mesmo em sangue (Fenton, 1992). Essa diversidade

coloca suas espécies em quase todos os níveis tróficos, atribuindo aos morcegos significativo papel no funcionamento dos ecossistemas. Dessa forma, populações, comunidades e guildas de morcegos possuem um amplo potencial enquanto provedores de serviços ecossistêmicos o qual tem sido destacado em sínteses recentes (Muscarella & Fleming, 2007; Kunz et al., 2011; Maas et al., 2016). A tabela S1 traz alguns exemplos de estudos que observaram e/ou quantificaram a contribuição de morcegos na provisão de serviços ecossistêmicos.

A diversidade de morcegos enfrenta ameaças, principalmente devido às pressões antrópicas de perda, fragmentação e degradação de habitat. No que tange a distúrbios guildas de morcegos apresentam respostas semelhantes (Medellín et al., 2000; Meyer et al., 2008; Farneda et al., 2015; Muylaert et al., 2016). Com isso, a tendência antrópica de conversão de ecossistemas naturais em coberturas simplificadas voltadas para o uso humano, faz com que a diversidade de morcegos seja perdida de forma não aleatória (García-Morales et al., 2013; Golçalves et al., 2017; Jung & Threlfall, 2018), caracterizando um típico padrão da defaunação antrópica (Young et al. 2016). Como consequência, paisagens fortemente alteradas abrigam comunidades funcionalmente empobrecidas e com baixo potencial de provisão de serviços ecossistêmicos. Considerando que a conversão de habitats nativos é uma realidade ubíqua nas regiões biogeográficas brasileiras (Mapbiomas, 2018) e produto das principais atividades econômicas (OEC, 2017), faz-se importante avaliar como o estado de desmatamento do Brasil tem afetado a diversidade e, consequentemente, o potencial de provisão de serviços por morcegos nas suas regiões.

Para tal, reunimos morcegos em grupos funcionais a partir da identificação de guildas tróficas (i.e. carnívoros, nectarívoros, frugívoros e insetívoros) e modelamos a distribuição de cada espécie. Em acordo com a teoria, atribuímos valores de

importância de provisão em relação às classes de tamanho (pequena – 1; média – 2; grande – 3), assumindo uma não equivalência funcional. Unimos as informações e produzimos mapas de distribuição da provisão potencial de serviços ecossistêmicos associados à fauna de morcegos. A provisão aqui é referida enquanto potencial pois não houve nenhuma quantificação da contribuição das espécies com os serviços (i.e. registro de interações, abundância relativa, etc). A escala do estudo e o número de espécies torna isso um enorme desafio. No lugar, uma métrica potencial foi aferida a partir dos valores atribuídos de importância de provisão (i.e. em relação ao tamanho corporal) e da adequabilidade ambiental resultante dos modelos. Esse valor de provisão potencial assume os seguintes pressupostos:

i)   Espécies ocorrem ao longo de toda sua distribuição projetada;

ii)   O de valor adequabilidade ambiental está relacionada a saúde das populações potencialmente presentes (i.e. proxy de abundância relativa, Ver Phillips et al. 2017);

iii)   Quanto maior a diversidade de uma dada região, maior a provisão potencial de serviços ecossistêmicos (Isso não unânime. Relações saturáveis podem ser identificadas onde um subconjunto de espécies suprem a demanda para o serviços. No entanto, a identidade das espécies nesse subconjunto podem variar ao longo tempo e espaço o que torna a provisão de comunidades mais diversa mais estável; Ver Kremen et al. 2002).

Compreendendo que paisagens nativas são os principais reservatórios de espécies (i.e. as potenciais ESP), incorporamos uma máscara de desmatamento aos mapas e avaliamos o quanto desse potencial foi perdido pela ocupação das regiões biogeográficas brasileiras (e.g. Amazônia, Mata Atlântica, Cerrado, Pantanal.

Caatinga e Pampa) e como cada guilda foi afetada. Aqui, adiciona-se o pressuposto de que os serviços têm origem nas áreas nativas (i.e. áreas conservadas servem de sistemas suporte para a manutenção de ESPs ,Ver Kremen, 2005). Para o trabalho, formulamos a hipótese de que carnívoros e nectarívoros, dada a maior sensibilidade à modificação de habitat, apresentariam perdas maiores em comparação a frugívoros e insetívoros, cujas espécies são mais tolerantes à perturbações. Conjecturamos também que dentro das guildas, a magnitude da perda de provisão potencial estaria associada ao tamanho corporal, com espécies grandes sendo mais afetadas em relação às espécies médias e pequenas (L> M> S).

Nossos resultados indicaram que as regiões biogeográficas brasileiras se diferenciam em seus valores de provisão potencial de serviços ecossistêmicos associados a morcegos, o que indica que as regiões reúnem diferentes composições de espécies e consequentemente, possuem potenciais para provisão de serviços ecossistêmicos distintos. As regiões se diferenciam também nos históricos de ocupação, o que resultou em diferentes magnitudes de perdas de áreas importantes para provisão (i.e. áreas de maior diversidade e assim, maior provisão potencial). Os resultados da análises de perdas para as guildas não corroboraram completamente com a primeira hipótese mas indicaram que o desmatamento afetou as guildas de morcegos diferencialmente e, consequentemente, a provisão de serviços. A segunda hipótese de que a magnitude das perdas de potencial de provisionamento está associada ao tamanho corporal foi corroborada, com morcegos grandes e médios apresentando maiores perdas que os pequenos. Este padrão foi observado em todas as guildas para o Brasil, quando todas as espécies de morcegos dentro de cada classe de tamanho foram consideradas.

Com isso, nossos resultados indicaram que espécies maiores foram as mais afetadas pela conversão de habitat. Isso indicaria que espécies potencialmente mais importantes para provisão desapareceram de mais áreas. A consequência funcional da perda dessas espécies em um sistema podem ser inúmeras. Em seus extremos estão a perda ou a manutenção da função (Tscharntke et al. 2005). A perda repentina do serviço indicaria que as espécies perdidas de fato possuíam um papel central na sua provisão, já a manutenção indicaria uma baixa contribuição prévia ou a capacidade de reorganização do sistema (i.e. resiliência). Grande parte dos estudos focam no serviço resultante da contribuição de todas espécies presentes (Williams-Guillén & Vandermeer, 2008, Maas et al. 2013; Maine & Boyles, 2015). Dessa forma, contribuições espécie-específica se tornam indistinguíveis e perguntas como "Quanta diversidade é necessário para provisão adequada do serviço", "Quais são as causa de variação na provisão?" e "Que espécies/características estão relacionados à eficiência de provisão" permanecem aberta.

Diante das incertezas sobre a dinâmica de provisão de serviços ecossistêmicos por morcegos no Brasil, conservação da diversidade de espécies nas guildas se torna a estratégia, dado que seu objetivo é assegurar resiliência. Para que possamos de fato usufruir dos serviços prestados por morcegos, é preciso entender como esses serviços são prestados e quem são esses prestadores. Muita atenção ainda deve ser direcionada para a elucidação dessas questões. Só quando for possível compreender a dinâmica de provisão de uma guilda que um plano de manejo para otimização de contribuições e para a conservação de seus serviços poderá ser desenvolvido. Para tal, é de extrema importância garantir a persistência dessas espécies e a literatura ecológica indica os caminhos cruciais para manter e impulsionar diversidade: restauração e conservação de habitat.

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Same pressure, different reactions: Ecosystem services by bats at risk in Brazil

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Abstract

Human activities have affected Earth's systems in an indiscriminate away and biodiversity loss has been the ubiquitous consequence. Along with the loss of species, ecological interactions once established are weakened or lost and ecosystem functions are changed or extinguished. Bats are a diverse group of mammals and are known to play significant roles in tropical ecosystems. The functional roles of bats have been associated with provision of ecosystems services. Bat diversity is currently being threatened by habitat loss and Brazil has a long history of converting naturally vegetated areas to farmland. Little is known about how habitat loss has affected bat functional diversity. Here we use species distribution models (SDMs) to assess the distribution of the functional diversity of Brazilian bats amongst Brazilian biogeographical regions. We used information on food preferences and body size to assigned species to guilds and functional groups. Habitat conversion impacts on providing guilds and groups were assessed for each Brazilian biome. Each region differed on their potential provision values and on history of land use conversion. This led to different proportional losses between bat groups, with no apparent general pattern. Negative impacts were strongest on larger species. Our results together with published information on bat's functional response to fragmentation highlight the possible current state of the ecosystems services provided by bats in Brazil's biogeographical regions. We provide recommendations for the safeguarding of bat functional diversity and highlight the urgency of further studies to adequately understand the underlying role of bats in providing ecosystem services in Brazil. Only then, effective management plans involving bats and the delivery of ecosystem services can be developed.

Key-words: anthropogenic pressure; Chiroptera; ecosystem services; functional diversity; habitat loss; species distribution models

Resumo

 Atividades humanas afetam os sistemas da Terra de forma indiscriminada e a perda da biodiversidade tem sido uma consequência ubíquia. Com a perda de espécies, interações ecológicas antes estabelecidas, são enfraquecidas ou perdidas e funções ecossistêmicas são alteradas ou extintas. Os morcegos são um grupo diversificado de mamíferos e desempenham papéis importantes em ecossistemas tropicais. Os papéis funcionais de morcegos têm sido associados a provisão de serviços ecossistêmicos. Sua diversidade está atualmente sendo ameaçada pela perda de habitat e o Brasil tem um longo histórico de conversão de áreas naturalmente vegetadas em terras agrícolas. Pouco se sabe sobre como a perda de habitat afetou a diversidade funcional dos morcegos. Aplicamos modelos de distribuição de espécies (SDMs) para avaliar a distribuição da diversidade funcional de morcegos brasileiros entre os biomas. Usamos informações sobre preferências alimentares e tamanho do corpo para atribuir as espécies a grupos funcionais provedores de serviços ecossistêmicos. Os impactos do desmatamento foram avaliados para o Brasil e cada região biogeográfica. As regiões diferiram em seus valores de provisão potencial e no histórico de conversão e dinâmica do uso da terra. Isso levou a diferentes perdas proporcionais entre os grupos de morcegos, sem um padrão geral aparente. Os impactos negativos foram mais fortes nas espécies maiores. Nossos resultados junto com informações publicadas sobre a resposta funcional de morcegos à fragmentação destacam o possível estado dos serviços ecossistêmicos prestados pelos morcegos nas regiões biogeográficas brasileiras. Há ainda muito a ser investigado sobre a conservação da diversidade funcional de morcegos e, diante o contexto, há uma urgência de estudos adicionais para compreensão adequada do papel efetivo de morcegos na prestação de serviços ecossistêmicos no Brasil. Somente então, planos de manejo que visem a conservação e a maximização das contribuições desse grupo poдererão ser desenvolvidos.

Palavras-chave: Pressão antropogênica**;** Chiroptera; serviços ecossistêmicos; diversidade funcional; perda de habitat; modelos de distribuição de espécies

Introduction

Throughout time, humans have been drivers of biodiversity change. Recently, anthropogenic disturbances have come to rival other environmental process in the shaping of Earth's systems - marking a new geological era known as Anthropocene [1]. Notably, existing systems are changing in an unprecedented way, with species extinctions happening at a rate 1000 times higher than what is naturally expected [2]. The human ecological footprint reach is such, that biologically and ecologically vast intact landscapes devoid of human disturbances are rare [3]. Alarmingly, 1 million species are predicted to face extinction within the next few decades, an amount thought to be catastrophic for the security, health and well being of the human population itself [4].

This grim picture did not come about due to lack of conservation efforts. Conservation Biology emerged as a crises discipline [5] traditionally focused on the conservation of taxonomic diversity. Despite the successes achieved, the approach was unable to halt the alarming rate of biodiversity loss. A more functional role for species recently gained the attention due to the discussion of ecosystem services [6]. In its essence, the ecosystem service framework directly embodies the human dependency on nature. A milestone for its development was the publication of the Millennium Ecosystem Assessment, which defined ecosystem services as any benefit people obtain from ecosystems, including direct and indirect services [7].

Undeniably, diversity is the driving force of ecosystem functioning. Consequently, along with the loss of species comes the disappearance of the ecological interactions evidenced by the extinct species or populations [8-9]. Changing the focus from taxonomic to functional diversity [10] simply means reducing the focus on species *per se* and instead considering a species' ecological

identity, and the services provided. For example, different co-occurring species may or may not perform similar ecological roles. If so, those with similar functions are functionally redundant [11], which means if one were to disappear, the ecosystem functioning would remain stable. At the same time, at the functional level, species might exist in such reduced populations that their interactions no longer have influence on the ecosystem, leading to what is referred as functional extinctions [12-13].

In terms of diversity, bats are an exceptional group to study. They are the second largest order of mammals in numbers, comprising more than 1386 species globally [14]. Currently, there are 182 species known for Brazil, representing 69 genera and 9 families [15]. Bats are abundant and form species rich communities in all Brazilian biomes. This characteristic is often related to the fact that they avoid competition through several mechanisms of niche segregation [16-19]. Through morphological and sensorial adaptations, bats are able to exploit many habitats and resources, feeding on fruits, insects, nectar, pollen, small vertebrates and even blood [20]. This places bats in nearly all trophic categories, giving them key roles in tropical ecosystems functioning. The functional role of bats in ecosystem is usually related to seed dispersal, pollination and arthropod and small vertebrates population control [21-23].

Although numerous, bat species face grave threats. Bats often exhibit species-specific responses to disturbances [24], but bat guilds are known to respond similarly to habitat loss and fragmentation. Carnivorous and nectarivorous species are sensitive to disturbances, with carnivorous species exhibiting low natural abundances, edge-sensitivity and rarely persisting in small fragments and matrix [25-27]. Nectarivorous bats, despite more abundant than carnivorous species, are associated with native and

intact areas, and respond rapidly to habitat loss [28]. On the other hand, frugivorous and insectivorous species are more tolerant of such disturbances due to their capacity to exploit resources present in disturbed and undisturbed areas [26, 28-29].

As such, the trend converting complex natural ecosystems into simplified land covers types, such as conventional agriculture and urbanization, bat biodiversity is lost in a non-random way [30-32]. As a consequence, landscapes that are heavily altered support functionally impoverished communities with low potential for provisioning the ecosystem services present there. Understanding how the provisioning potential of the Brazilian bat fauna is distributed is an important first step to the management of such services. In this study, we set out to map the potential distribution of the provisioning of ecosystem services associated with bats in Brazil.

We modelled the distribution of all bats known for Brazil and grouped them into feeding guilds of carnivore, nectarivore, frugivore and insectivore based on diet preferences described in the literature [33]. We also attributed differences in the provision of associated services in relation to functional redundancy and body size, with larger species explicitly assumed to be more important for provision in relation to their smaller counterparts that provide the same service. We combined all information and generated maps of provision potential of all ecosystem services associated to bats in Brazil, assessed how much of this potential has been lost through the historical occupation of natives biogeographical regions and how each guild was affected. We hypothesized that we would observe greater provision potential losses associated to the sensitive group of carnivores and nectarivores, and minor losses associated to the tolerant groups of frugivores and insectivores. In addition, we also hypothesized that within guilds, the magnitude of provision potential losses is

associated with body size, with large species being most affected in relation to small and medium sized species (L > M > S).

2. Methods

2.1 Species occurrence

We gathered occurrence data throughout all South American territory for the 182 bat species recognized to occur in Brazil [15]. Our dataset includes 40962 known geo-referenced localities, from which we derived 12466 records to describe the geographical distribution of Brazilian bats. This data set was assembled from museums vouchers, published literature and fieldwork done by the Laboratory of Bat Biology and Conservation at the University of Brasília, coordinated by LMS Aguiar. The additional the remaining 28496 records were obtained from the Global Biodiversity Information Facility – GBIF (http://www.gbif.org) to complement the data with the representation of bat records outside Brazil.

Taxonomic and spatial issues (errors on spatial coordinates or species names, for instance) were controlled for the collected dataset. We followed the taxonomic names adopted by Nogueira et al. (2018) [15]. Problems such as sampling bias and spatial auto-correlation are common in this type of data, and have been shown to interfere with model predictions [34]. In order to assess potential problems, we first calculated the Clark-Evans index, a point pattern analysis to determine data aggregation status [35]. When data clumping was evident, as for example, with occurrences of common and wide ranging species, a spatial filter of 10 km, maintaining only unique records for any locality within the set radius [36].

We performed an additional spatial thinning of the data, but now considering the distribution of point density along the map. Such strategies have been discussed in

articles that deal with the problem of sample bias [36-38]. Our method was based on the balanced design described at [34] and we used the R packages *dismo* [39] and *rangeBuilder* [40] to perform the following filters: first, a buffer of 50 km is created around each occurrence. Overlapping buffers are merged as one polygon and the number of occurrences in each one is then counted. Second, the mean density of the sampled area is calculated and buffers exceeding this value are listed. Finally, oversampled buffers are randomly resampled based on the number of occurrences needed to even the mean density. This procedure was meant to balance out the representation of sampled areas and to avoid over-representation of certain aspects of the environmental space due to artifacts of sampling bias. The treatments described above resulted in a dataset of 12058 occurrences, from which 128 species had sufficient records (considering a minimum of 10 occurrences for modelling) for distribution modeling.

2.2 Environmental variables

Environmental information was extracted from the bioclimatic variables available at the WorldClim database (http://www. worldclim.org) [41] to link our data. This widely used database represents interpolated data for past, current and future global climate. We first considered the 19 bioclimatic current variables at 2.5 arc min resolution, all derived from monthly temperature and rainfall values. Afterwards, correlation between pairs of variables was tested using the Pearson's test. Whenever a pair of variables showed values over 80% of correlation, only one of the variables was kept for each variable group, i.e., based on temperature values (bioclimatic variables 1 to 11) or precipitation (variables 12 to 19). This resulted on the selection of eight bioclimatic variables (BIO1, BIO2, BIO3, BIO4, BIO5, BIO12, BIO14 and BIO15 – see Table S3 for variables description), those which we

considered as having potential biological importance on limiting bat species'
distribution and that minimized correlation (Table S2).

2.3 Model building

We used MaxEnt software Version 3.4.0 [42] for modeling purposes because it
has the advantage of being a widely used, presence only algorithm that is flexible
enough to deal with multiple data realities [43]. Essentially, MaxEnt models a
species' distribution in the environmental space of the dimensions considered and
then projects it to the geographical space [44].

For model construction, we initially used the geographic extent of South
America and subsequently cropped the results to the boundaries of Brazil. As a
general rule, 10000 points were randomly sampled as background and we randomly
set aside 10-20% of the data for internal model testing. The test/training ratios
depended mainly on the amount of records available for model building. The latest
MaxEnt's complementary loglog (cloglog) output was used, which carries the same
advantages of the previous logistic output, but with greater theoretical support for its
interpretations [42 and 45].

We used a regularization multiplier of 2.5, a magnitude appropriate for the
fitting of more general models [46-47] and already used for the modeling of bat
species [48-50]. Finally, we assessed model accuracy with True Statistic Skill – TSS
[51] a threshold-dependent measure that is not affected by prevalence and validation
dataset size. It takes into account both omission and commission errors and ranges
from values of -1 to +1, where values below zero indicate a performance no better
than random. We established a TSS threshold value of 0.6 to determine whether a
model presented good predictive performance or not.

The described modeling process aimed to produce the best possible predictions with the data available. Each step included several theoretical assumptions of which we couldn't completely control for; for example the use of cloglog as MaxEnt output. This function comes from a recent interpretation of MaxEnt as an inhomogeneous Poisson process [42]. The Poisson process contains the assumption that the presence or absence of an individual of species A at a site is independent of the presence or absence of an individual of species B. That is, it disregards the possibility of any positive or negative spatial-correlation among species' occurrences.

Essentially, the inhomogeneous Poisson process assumption describes the concept of Grinnellian niche, where only environmental conditions limit a species' distribution [52]. Since bats are known to form diverse communities through mechanisms of niche segregation [16-19], where inter-specific competition is not seen as major limiting factor, they are fit with models for such assumptions. Due to this consideration, and to the controls performed for reducing sample bias, we believe we have an adequate base for the interpretation of our models as reliable distribution maps. Those of which were the bases for our ecosystem services analyses.

2.4 Provision potential of ecosystem services analysis

For each species a continuous map of values ranging from 0 to 1, indicating areas where species are potentially more likely to occur due to its environmental suitability was made. Each species was then grouped within a trophic guild. Afterwards, we separated each group into stacks for frugivores, insectivores, nectarivores, and carnivorous species. We refrained from treating omnivorous species as a separate category and instead placed them into one of the other guilds that their feeding is known to contribute to. For example, *Glossophaga soricina,* one of the

least specialized nectarivores bat, is classed as belong to the nectarivores', frugivores' and insectivores' species stacks.

We assumed a non-equivalency of provisioning between species even if having the same function based relative size of bats. We assume that larger are more important as providers of ecosystem services due to their capacity of exploiting a wider number of resources in a more intense fashion than their smaller counterparts [53-56]. In addition, within South America, bigger bat species are less numerous and thus, likely perform less redundant ecosystem functions.

Our approach was to use mean forearm length as a proxy for body size. We gathered from the literature data on forearm measurements for all 182 species occurring in Brazil. For each trophic group, with a k-means clustering analysis, we identified forearm lengths at intervals that represented small, medium and large categories. These were then attributed values of 1, 2 and 3, respectively. Subsequently, we multiplied each distribution map by the species' body size category value. This resulted in an increase of different magnitudes on a species' distribution according to its relative size. This was followed by summing of the maps of each feeding guild, which then had their scale values standardized to enable comparisons. We produced five maps (Frugivorores (FR), Insectivores (IN), Nectarivores (NEC), Carnivores (CA), and All bats (ALL), scaled from 0 to 1. These incorporated information on the environmental suitability of sites and species provision values (named as Maps of Potential Provision)

In addition, we included the current state of habitat conversion of the Brazilian territory to our analysis using the 2017 MapBiomas version 3.1 land cover map (http://mapbiomas.org/). The map is presented at a 30 m resolution and includes several land cover features. From it, we created a binary map of natural vegetation

remnants. First, we resampled the map to a resolution of 1 km^2, making it compatible with the distribution models. Water bodies' were classed as non-valued so it wouldn't interfere with the analysis of potential provision loss. Finally, we multiplied our maps of potential provision to our binary vegetation fragments remnants mask to incorporate deforestation.

To estimate potential provision loss, we compared in terms of frequency of cells of attributed low, medium and high potential provision values for all bats and for each feeding guild before and after habitat conversion. With such, we could observe how the historical habitat loss has affected the potential provision of the ecosystem services associated with bats in Brazil and for each biogeographical region. To quantify habitat loss for each biome, we identified classes of low, medium and high potential provision for each feeding guild, relative to their distribution of values in the region. Number of cells of each class were summed prior and after land conversion and differences recorded. Areas of medium and high potential provision were identified as important areas for provisioning. The classification of intervals was done with ClassInt Package in the R software [57].

To test our hypothesis we used a binomial proportion test (two proportions z-test). Proportion tests were performed between guilds to see whether we would observer a gradient of losses following the expected pattern of carnivory > nectarivory > frugivory > insectivory. Another set of tests were performed between size classes within guild and within all bats to ascertain whether proportional losses were associated to bat's body size in the respective order: large > medium > small. All analyses were done in the R software [58].

3. Results

3.1 Bat's SDMs and classification

For the 128 species, we generated 113 generated models with good predictive performance. TSS values ranged from 0.6 to 0.97, with 53 species validated with scores between 0.6 and 0.69 and 60 species validated between 0.7 and 0.97. Five species were removed from the study due to unsatisfactory model results after a visual inspection. Thus, all results presented here are based on 105 modelled bat species, of which 65 were identified as insectivores, 28 as frugivores, 12 as nectarivores and three as carnivores (Table S4).

Three mean forearm lengths intervals for each trophic group resulted from the unsupervised classification of body size by k-means clustering resulted into three mean forearm lengths intervals for each trophic group analysed (Table 1). Overall, there were 52 small, 38 medium and 16 large bat species. Size differences were most marked for insectivorous and frugivorous bats (Table 1). Overall, for all groups with the exception of carnivores, most species within each guild were classified as small (Table S4).

Table 1. Forearm length intervals corresponding to small, medium and big size classes for each trophic group considered. Groups were obtained by an unsupervised kmeans classification.

| Classes | Forearm length (mm) | | | |
	Insectivory	Frugivory	Nectarivory	Carnivory
small (1)	[28.5, 42)	[28.5, 41.5)	[30.7, 36.2)	[61.5, 71)
medium (2)	[42, 56.85)	[41.5, 54)	[36.2, 39.4)	[71, 93)
large (3)	[56.8, 80]	[54, 71.5]	[39.4, 40.3]	[93, 101]

3.2 Potential provision of ecosystem services associated to the bat fauna in Brazil

For Brazil and each biogeographical regions, values of corresponding low, medium and high potential provision were identified (Table 2). The spatial distribution of theses potentials for Brazil can be viewed in Figures 1 and 2. The Pantanal (freshwater wetland) presented the highest potential provision scores for services associated to insectivory and carnivory, whereas the Amazon and Caatinga (tropical rainforest and seasonal dry forest, respectively) exceeded the other regions in terms of potential provision for services associated to frugivory and nectarivory, respectively. The Atlantic Forest and Cerrado (tropical rainforest and woodland savannah, respectively) exhibited intermediated values of potential provision, indicating that these biogeographic regions are important for safeguarding the variety of services associated with bat diversity. Finally, the Pampa region (southern grasslands) exhibited the lowest values for all categories of services, except for insectivory, which was not exceeded only by the Amazon region.

Table 2. Potential provision intervals of services associated with bat's feeding guilds in Brazil and in each biogeographical region.

	All bats			Frugivory			Insectivory		
	Low	**Mid**	**High**	**Low**	**Mid**	**High**	**Low**	**Mid**	**High**
Brazil	[0.591,1.930)	[1.930,2.518)	[2.518,3.778]	[0.096,0.499)	[0.499,0.732)	[0.732,1]	[0.120,0.465)	[0.465,0.630)	[0.630,1]
Amazon	[0.788,1.797)	[1.797,2.168)	[2.165,3.226]	**[0.436,0.694)**	**[0.694,0.836)**	**[0.836,1]**	[0.120,0.385)	[0.385,0.477)	[0.477,0.769]
Cerrado	[1.484,2.105)	[2.105,2.508)	[2.508,3.483]	[0.265,0.527)	[0.527,0.670)	[0.670,0.874]	[0.329,0.512)	[0.512,0.635)	[0.635,0.875]
Caatinga	[1.430,2.110)	[2.110,2.653)	[2.653,3.702]	[0.147,0.383)	[0.383,0.537)	[0.537,0.896]	[0.329,0.509)	[0.509,0.654)	[0.65,0.925]
Atlantic Forest	[0.868,1.986)	[1.986,2.839)	[2.839,3.778]	[0.189,0.448)	[0.448,0.642)	[0.642,0.997]	[0.220,0.584)	[0.584,0.753)	[0.753,1]
Pantanal	[2.326,2.653)	[2.653,2.870)	[2.870,3.242]	[0.353,0.520)	[0.520,0.606)	[0.606,0.827]	**[0.574,0.734)**	**[0.734,0.813)**	**[0.813,0.946]**
Pampa	[0.591,1.064)	[1.064,1.525)	[1.525,2.540]	[0.096,0.188)	[0.188,0.261)	[0.261,0.454]	[0.374,0.508)	[0.508,0.608)	[0.608,0.803]

Table 2. Cont**.**

	Nectarivory			Carnivory		
	Low	**Mid**	**High**	**Low**	**Mid**	**High**
Brazil	[0.035,0.412)	[0.412,0.645)	[0.645,1]	[0.078,0.478)	[0.478,0.668)	[0.6681137,1]
Amazon	[0.089,0.337)	[0.337,0.489)	[0.489,0.850]	[0.131,0.406)	[0.406,0.522)	[0.522,0.782]
Cerrado	[0.256,0.588)	[0.588,0.720)	[0.720,0.979]	[0.339,0.510)	[0.510,0.666)	[0.666,0.922]
Caatinga	**[0.463,0.651)**	**[0.651,0.803)**	**[0.803,1]**	[0.299,0.5203)	[0.520,0.683)	[0.683,0.984]
Atlantic						
Forest	[0.082,0.395)	[0.395,0.655)	[0.655,0.989]	[0.130,0.501)	[0.501,0.732)	[0.732,1]
Pantanal	[0.324,0.505)	[0.505,0.622)	[0.622,0.809]	**[0.575,0.765)**	**[0.765,0.854)**	**[0.854,0.965]**
Pampa	[0.035,0.160)	[0.160,0.302)	[0.302,0.626]	[0.078,0.235)	[0.235,0.397)	[0.397,0.657]
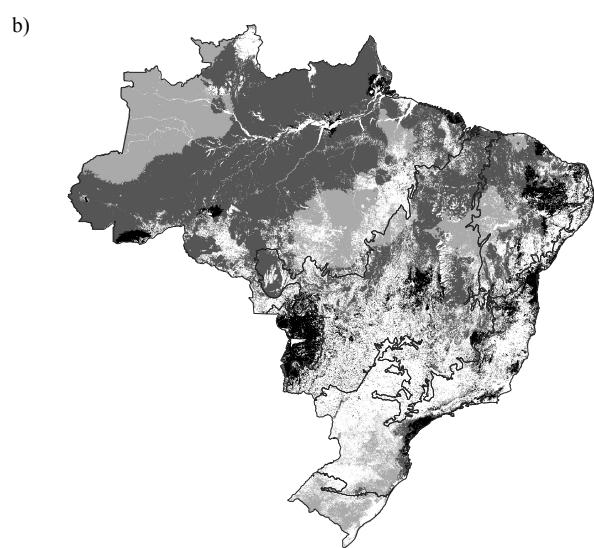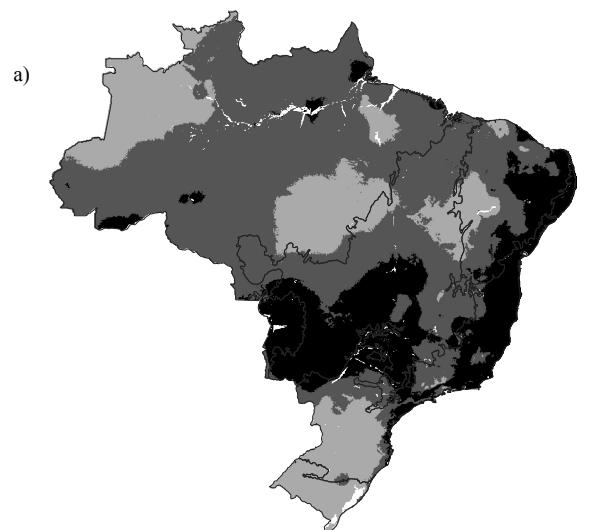
Fig. 1. Distribution of the potential provision **for all bat species in Brazil prior to (a) and after deforestation (b).** Black, dark gray and light gray correspond to areas with high, medium and low potential provision. Lines represent a biogeographical region limits. White areas represent water (a) and habitat conversion (a and b).
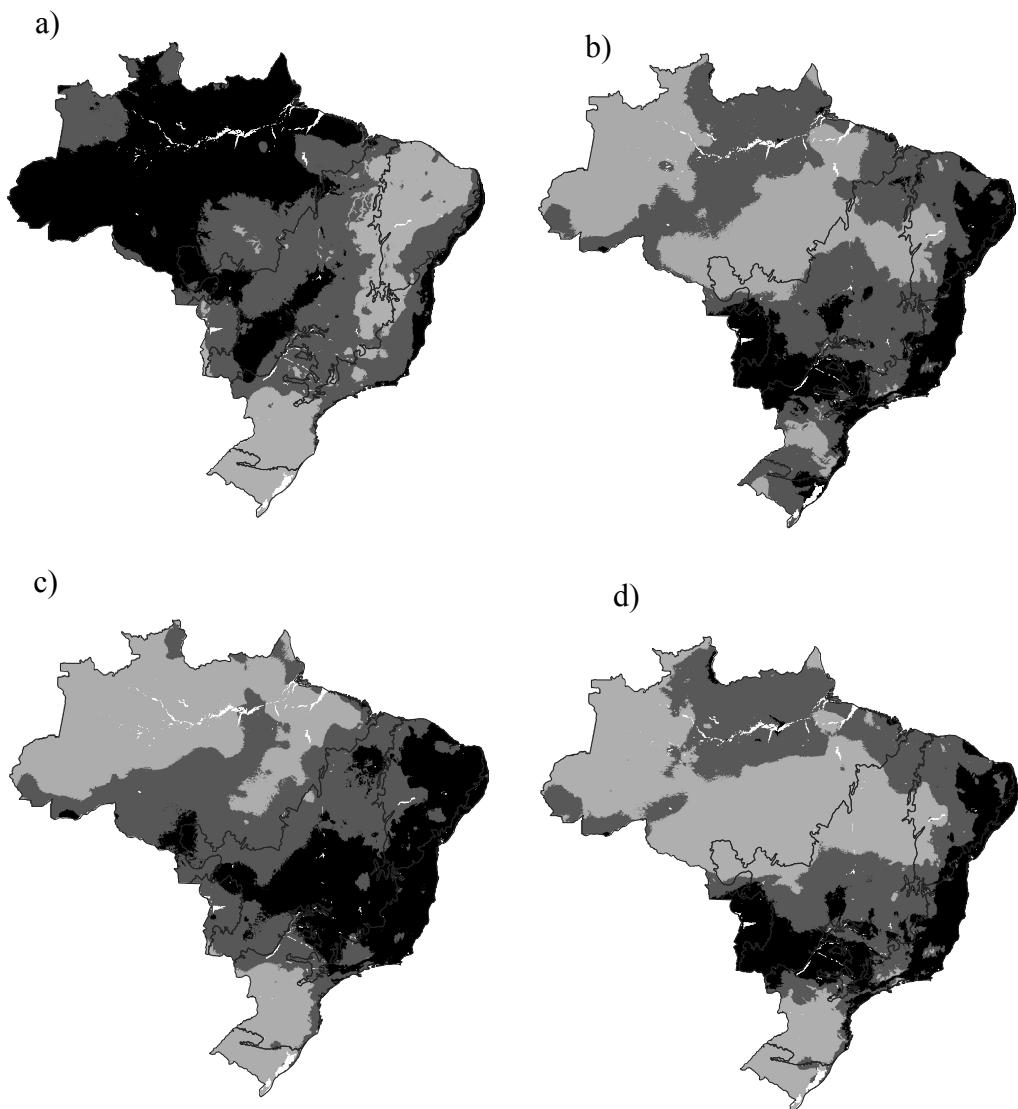
Fig. 2. Distribution of the potential provision **associated with each bat feeding guild for Brazil.** Black, dark gray and light gray represent high, medium and low potential provision Lines represent a biogeographical region limits. a) Carnivory b) Nectarivory, c) Frugivory and d) Insectivory.

Knowing the potential provision scores for a country or region it's not the only way of assessing a place's likelihood of providing specific ecosystem services. Another complementary approach is to see how these values are distributed in space (Table 3). When comparing proportions of important areas for provisioning of ecosystem services we found that the provision potential of the same services are differentially represented across biogeographical regions (z-test $p < 0.05$, See S6 for R *script for tests results*).

Table 3. Potential proportion (%) of important areas for provisioning of ecosystem services associated to bat diversity in Brazil and in each biogeographical region.

	Frugivory	Insectivory	Nectarivory	Carnivory	All bats
Amazon	0.804	0.764	0.615	0.667	0.830
Cerrado	0.756	0.644	0.719	0.617	0.810
Caatinga	0.682	0.750	0.695	0.749	0.729
Atlantic Forest	0.710	0.677	0.712	0.731	0.719
Pantanal	0.795	0.897	0.860	0.772	0.775
Pampa	0.762	0.649	0.562	0.816	0.765
Brazil	0.810	0.636	0.645	0.549	0.771

3.3 Ecosystem services potential provision losses

With the historical occupation of Brazilian biogeographical regions, much of the potential provision was lost. The Atlantic Forest region is an extraordinary case, with a total loss of approximately 70% of its area. This impacted 76% and 64.3% of areas with a medium and high potential provision, respectively (See S5). This reduced the area providing ecosystem services from 71.9% (Table 3) to 20% of Atlantic forest's native vegetation (Table 4). The Cerrado region follows Atlantic Forest with about 50% loss of its native vegetation cover, with areas of high potential provision being the most affected (70.7%, See S5). Presently, only 36.6% of important areas for ecosystem services provisioning remain vegetaded.

Intermediate magnitudes of habitat conversion are found in the Pampa and Caatinga region. Approximately 41.4% of the Pampa's native vegetation was removed, with important areas for provisioning being the most affected (46.1% of areas with high and 44.1% of areas with medium potential provision). Prior vegetation conversion, 76.5% of Pampa was covered by important areas of ecosystem

services provisioning. After conversion this potential was reduced to 42.2% of Pampas native vegetation remnants (Table 4). For the Caatinga, approximately 35% of it has been converted to other land uses. This impacted 57.17% of areas with high and 32.4% of areas with medium potential provision (see S5), which resulted in a 72.9% to 43.1% reduction of important areas for provisioning (Tables 3-4).

Despite the significant difference in geographical extent, proportionally, the Pantanal and Amazon are the biogeographical regions that have been the least impacted by of habitat conversion. The Pantanal's loss sums to 23% of its native cover, with areas of low and medium potential provision (36.4 and 20.69%, respectively) mostly impacted. Comparatively, this caused a less drastic decrease in the representation of important areas for provisioning, which went from 77.5% to 62.4% (Tables 3-4). Finally, the Amazon region has accumulated a loss of 15.6% of its native cover. This represented a relatively balanced loss across important areas for provisioning (19.96% of medium and 14.48% of high potential provision), which resulted in the drop of important areas' representation from 83% to 68.9% (Table 3-4).

Table 4. Current proportion (%) of important areas for provisioning of ecosystem services associated to bat diversity in Brazil and in each biogeographical region after habitat conversion.

	Frugivory	Insectivory	Nectarivory	Carnivory	All bats
Amazon	0.707	0.630	0.473	0.575	0.689
Cerrado	0.353	0.261	0.334	0.239	0.366
Caatinga	0.408	0.454	0.408	0.452	0.431
Atlantic Forest	0.186	0.193	0.208	0.201	0.200
Pantanal	0.601	0.731	0.661	0.637	0.624
Pampa	0.421	0.341	0.325	0.453	0.422

Brazil	0.551	0.598	0.373	0.321	0.499

3.4 Bat's feeding guilds responses to habitat conversion

The binomial proportion test performed between guilds didn't show the expected pattern of magnitude of loss across the different functional groups, therefore the hypothesis that we would observe greater losses for carnivorous and nectarivorous species, and minor losses for frugivorous and insectivorous was not supported. In fact, the analysis showed a lack of pattern about how trophic groups were affected in each region, with guilds varying from positions of most affected to intermediate and least affected (Table 5). Nonetheless, when all bats within each guild were considered (i.e. the whole ensemble of Brazilian bats from each gruild), we found some support for the hypothesis as nectarivores and carnivores were the most affected by habitat conversion and insectivores and frugivores were the least.

With the exception of the impact felt by the potential provision of frugivory and carnivory in the Pampa region, all differences in the proportional loss of important provisioning areas were significant, which indicates that habitat conversion has affected the potential provision of guilds differentially across Brazil.

Table 5. Values of proportional loss of areas with important potential provision of ecosystems services associated to bats of each feeding guild and the order of magnitude of loss. Significance was obtained with a z-test of proportions.

	Carnivory	Nectarivory	Frugivory	Insectivory	Order of impact	P-value
Amazon	0.137	0.231	0.120	0.175	NEC > IN > CA > FR	< 0.05
Cerrado	0.612	0.535	0.532	0.594	CA > IN > NEC > FR	< 0.05
Caatinga	0.396	0.411	0.401	0.393	NEC > FR > CA > IN	< 0.05
Atlantic F.	0.725	0.707	0.737	0.714	FR > CA > IN > NEC	< 0.05
Pantanal	0.175	0.230	0.242	0.185	FR > NEC > IN > CA	< 0.05

Pampa	0.443	0.420	0.447	0.474	IN > FR = CA > NEC	< 0.05
Brazil	0.415	0.420	0.319	0.414	NEC > CA > IN > FR	< 0.05

3.5 Responses of different body size classes to habitat conversion

With the exception of carnivores, when proportional losses were compared for Brazil as a whole, all cases showed greater provisioning losses linked to large and/or intermediate body size species, and minor losses associated to small bats (Table 6, See Table S7 for proportions).

Potential provision losses linked to large and medium sized carnivorous bats were the same, with no statistically significant differences in all biogeographical regions. For nectarivorous species, in the Pampa and Pantanal, small bats experienced greater losses then their larger counterparts, with intermediate losses in the Cerrado, Caatinga and Atlantic Forest and minor losses only in the Amazon. In the case of frugivorous bats, small and medium sized species were the least and most affected depending on the region (Table 6). A different trend was observed for insectivores, where small bats mainly occupied intermediate positions of provisioning loss, with the exception of Cerrado, where small insectivores were the least impacted by habitat conversion. Distinctively, large insectivores were the least affected in most regions, whereas medium size bats were the most (Table 6).

The hypothesis that magnitude of losses of potential provision is associated with body size was corroborated, with large and medium size bats showing greater losses than small bats. This pattern was observed on all, with the exception of carnivores, feeding guilds for Brazil, when all bat species within each body size class was considered.

Table 6
Order of magnitude of impact when comparing losses from small, medium and larges of each guild. Highlighted results are those in alignment with the hypothesis. Significance was obtained by z-test of proportions.

	Carnivory	Nectarivory	Frugivory	Insectivory	All bats	p-value
Amazon	L = M	M > L > S	M > L > S	M > S > L	M > L > S	p < 0.05
Cerrado	L = M	L > S > M	M > L > S	M > L > S	M > L > S	p < 0.05
Caatinga	L = M	L > S > M	M > L > S	M > S > L	M > S > L	p < 0.05
Atlantic F	L = M	M > P > L	P > M > L	L > S >M	S > L > M	p < 0.05
Pantanal	L = M	S > M = L	P > M > L	M > S > L	S > M = L	p < 0.05
Pampa	L = M	S > L > M	L > M = S	L > S > M	L > M = S	p < 0.05
Brazil	L = M	**L > M > S**	**L > M > S**	**M > L > S**	**L > M > S**	**p < 0.05**

L = Large
M = Medium
S = Small

4. Discussion

Brazil has experienced extensive conversion of its biogeographical regions over recent decades [59] and this resulted in a significant loss of bat's ecosystem services potential provision. More than 70% of Brazil's territory once maintained important areas for provisioning of ecosystems services associated with bats. This land use change, mostly affected areas of medium and high potential provision for bats within regions, which resulted in a 27% reduction of these areas across Brazil. Each biogeographical region contained its own potentiality for ecosystem services provisioning and its own history of land occupation, and thus contributed differently to this depletion process.

4.1 The potential provision of Brazilian biogeographical regions, losses and possible implications

The Atlantic Forest is an important and well-studied Brazilian biogeographical region. It once occupied 150 millions ha, but now is reduced to thousands of small fragments accounting for about 12% of its original coverage [60]. The region's current dominant land use is large-scale sugarcane farming and cattle ranching [62]. In addition, it concentrates 56% of Brazil's urban areas [62]. Consequently, there was an extensive loss of potential provision for all bat's trophic groups. Any remaining provisioning of ecosystem services by bats in the Atlantic Forest experiences the ubiquitous influence of habitat fragmentation, a factor known to impact species abundance and the structure of bat assemblages [63].

In a fragmented Atlantic Forest in Paraguay, landscapes with different composition and configuration showed different impacts on the bat guilds present [29] Carnivorous species abundance was associated with highly forested areas. Similarly, nectarivorous bat species were associated with large and less fragmented forest patches, whereas many frugivorous species benefited from different various levels of fragmentation. It has been shown that species richness of frugivorous bats peaks at intermediate amounts of forests in the landscapes [28], suggesting that frugivory by bats is a relatively stable function. Although our results showed the greatest losses for bats in this trophic level, ecosystem services associated with frugivory by bats can still be occurring in many parts of Atlantic Forest [64]. As for the carnivores' trophic class, services provided by these bats are likely very restricted in the region. Although nectarivory suffered only minor losses it also likely that this provision is concentrated around larger and less isolated forest fragments, limiting the areas where services by this group can be effectively delivered.

Cerrado is the second largest biogeographical region in Brazil and is considered to be the most biodiverse Neotropical savanna in the world [65]. Our results indicate that important areas of provisioning are concentrated in the central and southern region of the biome. These are the most deforested areas of the region with large concentration of conventional agriculture (e.g. monocultures of soy and sugarcane) and cattle ranching [60]. Agriculture accounts for more than 50% of Cerrado's original extant. Although Cerrado supports more native vegetation remnants than the Atlantic forest, less than 3% of the area is designated as protected areas [66]. This pattern of anthropogenic activity in Cerrado has impacted about 70% of areas with high provisioning potential of all bats.

Carnivorous bats suffered the greatest losses of important native vegetation areas for provisioning, with remaining areas occurring as fragments surrounded by agricultural matrix. This context likely hampers this bat trophic level from exerting vertebrate population control services in these regions. Carnivorous bat species abundance increases with amount of Cerrado area in fragmented landscapes [28]. These species are also edge-sensitive, exhibit low mobility and do not benefit from high contrasting patch-matrix environments unless in proximity to continuous forest [26]. Thus, carnivory is likely a threatened service the Cerrado.

Insectivorous bats represented the second greatest loss category of provision areas in Cerrado. These bats are abundant and generally are the least affected by habitat conversion towards agriculture and pasture. This is related to their capacity of using these open areas for hunting, hence their recognition as pest controllers [67-69]. This tolerance and their ability to forage in open spaces can be different between species owing to aspects of wing morphology [31] call structure and roost requirements [32]. Nevertheless, the provision of ecosystem services linked to

insectivorous bats may be considered as redundant due to the high number of species performing it.

Nectarivory was not among the most affected services, but is noteworthy. In the Cerrado region bats are key pollinators of economically important plants such as *Caryocar brasiliensis* [70] and many other common species [71]. There are 14 predominately nectarivorous bats in Brazil [72] with only a subset of these occurring in the region. Two of these are listed as threatened: *Lonchophylla dekeyseri* and *L. bokermanni* [73-74]. Both exhibit restricted ranges and while mainly threatened by habitat loss, populations also experience mortality due to vampire bats control activity [75-76]. Considering the number of nectarivory provider species, their responses to habitat degradation [28] and the restricted nature of this service, this service will likely be threatened.

Caatinga is a tropical dry forest of semi-arid climate with predominantly thorn-scrub vegetation. It's a region of extreme variation in rainfall and for the most part of the year suffers a water deficit [77]. There is a significant human population residing in Caatinga that rely heavily on subsistence agriculture, goat husbandry and firewood harvesting [78]. Caatinga is also a region supporting extensive areas planted with export-oriented monocultures of fruit [61]. These crops demand high levels of water for productivity, an already scarce resource for Caatinga. Agricultural development has led to the deforestation of a great part of the biogeographical region and to the degradation of remaining habitats, leading to desertification [79].

For Caatinga, deforestation culminated in the loss of 57.2% and 32.4% of areas with high and medium potential provision by bats. That means that large areas with significant bat diversity have been impacted by habitat loss. Our results also indicated that Caatinga is the nectarivory capital of Brazil, holding the highest scores

of provision potential for pollination services. Bats pollinate 13.1% of the local flora, making them the third most important group of pollinators in the region losing only to medium-large bees and hummingbirds [80]. Alarmingly, this group experienced the largest proportional losses, losing 41.1% of important areas for provisioning. Phytophagus (nectarivorous and frugivorous) bats are usually the most abundant in the local assemblages throughout the year [81-83], but this pattern may change with abnormal seasonal events such as longer periods of drought [84]. This means that, even if the conversion of Caatinga's vegetation stopped, nectarivory would still be threatened by events of climate change. Projections already points for such scenario, with Caatinga becoming increasingly an arid biogeographical region [85].

Frugivorous bats were also amongst the most affected groups by habitat loss in Caatinga. These species are one of the most abundant trophic groups in the region and possibly important agents of long-distance seed dispersal as have been shown in other semiarid regions [87-88]. Interestingly, frugivores in Caatinga don't seem to benefit from intermediate disturbances situations as if they do in rainforests [84]. Firewood collecting is one of the main causes of Caatinga deforestation [61], and mostly impacts native-wild fruit trees [89-90]. It has also been demonstrated that in Caatinga medium and large body frugivorous bats depend on humid enclaves, known as cloud forests, for resources during the dry season [83]. The destruction of these humid refuges threatens the persistence of these species, and may affect the dispersal of larger fruits bearing tree species. With time the connectivity between humid and dry parts of the region may be reduced, jeopardizing bat and plant diversity.

The Pampa was the biogeographical region with the lowest provision potential score in Brazil, with the exception of its values associated to insectivory. The lower scores were expected, since the Pampa is a natural grassland of subtropical climate. It

also marks the latitudinal limit for the distribution of many bat species. This region mostly sustains Phyllostomidae, Vespertilionidae and Molossidae bats [90]. Due to environmental characteristics here, insectivory should be the dominating services group, but is unlikely that its potential provision in Pampa is higher than it is in the Amazon. This is likely an artefact produced by the models since MaxEnt showed a tendency of overfitting (i.e. closely matching prediction to input data). The Amazon's pattern of occurrences were less numerous and spatially more sparse. This seemed to weaken predictions for the area, even with the use of higher beta-regulation and balanced spatial filtering [91].

The Pantanal is an extensive floodplain surrounded by the Cerrado, Chaco, Amazon and Atlantic Forest. It is one of the least impacted biogeographical regions in Brazil and one of the last wetland environments in the world that wasn't destroyed by habitat conversion [92]. It holds one the richest mammal faunas in the country, forming diverse communities with significant presence of large vertebrates [93]. Bats account for 40% of this fauna [94]. Overall, Pantanal presented high values of ecosystem services provision for all groups and also the highest for insectivory and carnivory, which were amongst the least impacted groups. These high values reflect a the presence of species typically from neighbouring biogeographical regions (e.g. Cerrado, Amazon and Atlantic Forest). The Pantanal supports diversity due to its significant amounts of forest and savannah habitats mosaics and water availability [95]. Bat surveys in the Pantanal's floodplain show a marked dominance of insectivorous species [96-97].

The Pantanal is surrounded by the upland areas of the Paraguay River basin, a region extensively occupied by agriculture. The Pantanal's degradation through land use change thus has been happening from outside its borders, in the headwaters of

their main river basins, by the spill over of cattle ranching. These changes mostly affected frugivorous and nectarivorous species, which have lost 24.2% and 23% of their respective important areas. Frugivory in the Pantanal is characterized by high overlap of resources among species, indicating little diversity of fruit resources for bats in the region [96-98]. Nonetheless, frugivorous species form a well-represented group in Pantanal with *Artibeus planisrostris* being the most abundant [96]. This is a large Phyllostomidae that utilize the biogeographical region's entire range of habitats (i.e. floodplains and uplands) evenly and thus, acts as an effective seed disperser [100]. Undoubtedly, the Pantanal still maintains well-preserved bat assemblages with great potential for ecosystem services provisioning.

Potential provision values for the Amazon are likely underestimating the true potential of bats in the largest rainforest in the world. This could be a product of only a few highly sampled areas that already register great diversity and large less studied areas [101]. This sparse distribution of bat occurrences led models to the favour the more intensively surveyed areas elsewhere. The Amazon contains the highest diversity of bats, with estimations of 124 species present [102] and with great presence of rare species. Our results indicate that Amazon is the capital of Brazil for frugivory, with Phyllostomidae commonly dominating forest assemblages [103-104] and playing important roles in tropical rainforests. In forests of Panama, for example, these bats have been associated to interact with 53 plant species [105].

Native vegetation conservation efforts in Brazil have been biased towards forest protection [106]. Of the 713 federal integral protection areas, 128 areas are in the Amazon accounting for about 10% of its territory. This region harbours large areas of forest buffered from damaging exploitation [141]. As such, most of the Amazon's deforestation is concentrated on its borders, a region known as

deforestation arc. Pastures for beef production are predominant and are the main cause of deforestation [61], but the Amazon also faces significant pressures from logging, mining and large-scale agriculture.

As a result of its large size and of its high amounts of vegetation remnants proportions, the Amazon is the least impacted biogeographical region in terms of proportional losses of the potential provision of bats. Nectarivorous were the most affected group, followed by insectivorous, carnivorous and frugivorous species.

Loss of functional traits with deforestation and fragmentation was observed by many studies led in the region [27, 108-110]. Bat's body mass and trophic level were the important predictors of bat vulnerability in the Amazon [27]. Small phytophagous species dominated small fragments and matrix environments, whereas carnivorous species showed high associations with old-growth continuous forest, rarely occurring in fragments. Furthermore, through secondary forest regrowth and attenuation of fragment-matrix contrast, functional recovery of groups has been observed [110]. This temporal process of matrix regeneration increased functional richness and redundancy of the bats communities using these areas through the arrival of species performing different ecological roles [109]. These findings suggest the importance of preservation of large tracts of forest, since these are the ones truly safeguarding biodiversity and serve as a healthy source for the recolonization of recovering areas.

4.2. Are we losing services?

For Brazil, our results indicated a relation between magnitude of loss and bat body size. With the exception of carnivores, larger bats showed greater losses than smaller bat species for all remaining groups. This means that, when considering the whole Brazilian ensemble of bats for each guild and for all bats, those with larger bodies disappeared from a greater number of areas. According to our approach, this is

the highest potential provision loss a region could suffer; given that bigger species are rare (in number of species), potentially perform more unique functions and attained greater provisioning importance.

Despite the inherent subjectivity of any classification approach, grouping bats into body size classes is a common practice in bat studies [117] Information on forearm length is more readily available for bat species than full body length measures. It is also a conservative measure known to correlate with body mass [118] Thus, using forearm length as a proxy of bat body size is an appropriate method [54, 118-119]. Bat research has a long history of studies relating form to function [23, 112-114]. Body size influences the use of resources, with bigger bats being able to use a wider diversity of resources and with greater intensity [53-56, 114-116 and 121] Although it remains to be tested, relating body size to functional influence is a logical and theoretically sound assumption [128]. These aspects are expected to differentiate bigger and smaller bats in terms of function or, in other words, on how each group potentially participate in the ecosystem service provision.

Studies on bat's provision of ecosystem services have mainly focused on the aggregate function (i.e. the service(s) resulting from the ensemble of ESP present; [124]). A common practice for the studies of pest suppression is the use of exclosure experiments [22]. While these studies offer important insights on local diversity impacts on crop yield and quality [129-131], little light is shed on the dynamics of provision. Even with the aggregate service measure at hand (e.g. fruit sets, plant damage, etc.) questions of how much diversity is needed for the desired outcome or which species/traits are related to effectiveness of service delivery remain unanswered. As such, these results offer evidence for service existence while making

good cases for conservation of bat diversity as a whole, accounting for the importance of maintaining multiple species contributions to a service [132].

Conservation of guild diversity is an important precautionary approach to ecosystem services in front of uncertainties in the dynamics of provision since and it aims to secure function resilience [133]. Function resilience implies redundancy, which in turn, implies replacement among species [134]. Through our classification, potential for redundancy (i.e. number of species for replacement) decreases with body size. This is a pattern observed on mutualistic networks [135]. What it means is that the local loss of bigger species, if they do have relative greater functional importance, should come with greater functional consequences due to reduced resilience and to the limited possibility of compensatory responses from other species; and this should be accompanied by rapid function loss [124].

In cases of redundancy, the very own capacity of bats population to respond in a compensatory way should be questioned. Neotropical bat communities are not consistently structured by competitive interactions [136] and bat species are long-lived organisms with low fecundity [137]. Thus, bats are likely not responsive to population fluctuations and not capable of the rapid growth such compensatory responses require. Instead, due to their high mobility, function stability might depend on a rescue effect from surrounding populations suggesting the importance of the conservation of biodiversity on a landscape scale [138], as observed by [109].

Beyond redundancy, guild diversity can also enhance function through mechanisms of species complementarity [139]. Bats exploring similar resources seem to separate their uses in space and time (i.e. resource partitioning) [16-19]. Species performing similar functions at different spatial-temporal scales provide resilience to ecosystem services [120], reiterating the importance of conserving bat diversity as a

whole. Nevertheless, it's a fact that species differ in their potential contribution to ecosystem services and body size could be a trait dictating this in bats, as it is on other vertebrates [140]. If such, it is also a well-established response trait indicating vulnerability to disturbances such as fragmentation [117 and 27]. Identifying potential key provider species' and their contributions to aggregate function is crucial for our understanding of the dynamics ecosystem services provision by bats under changing environmental conditions.

5. Concluding remarks

5.1. Researching and managing bats for ecosystem services

Our results showed how the potential for provision of ecosystem services associated to each bat guild considered is differentially distributed across Brazil, how each biogeographical region holds different species assemblages providing such services and how these groups are being affected by habitat conversion. If assemblages differ, it is likely that species contribution also differ between regions. Which species are the key ecosystem service providers in forest and open area biomes? Is aggregate function in high diversity areas different from those found in less diverse areas? How land use affects aggregate function? The answer to those questions will lead to our further understanding on how bats contribute to ecosystem services across Brazil and how our interventions on the landscape have been affecting such contributions.

Pinpointing Brazilian bat's contribution in the provision of ecosystem services was beyond the scope of this paper. In fact, studies assessing more quantitatively the role of bats in their provision are lacking in Brazil. Bat's potential as pest controllers have propelled significant research efforts [22] but have been virtually ignored in

Brazil [122]. Effective management will only be possible once enough research is directed towards understanding the underlying role of bat species as ecosystem services providers [123]. Although it can be extremely challenging to quantify species population's contributions to a service [140], existing frameworks suggest that management could be facilitated by the use of already collected data on species ecology and habitat requirements for the identification of the ecosystem service's supporting systems (i.e. habitat requirements for the support of services providers) [124].

Published literature on bat's habitat use point directions for improving local bat diversity and activity, if this is associated to an improvement on bat's aggregate function remains an open question. An important first step for safeguarding bat services is to sustain their supporting systems, mainly by increasing the amount of native area and stopping indiscriminate habitat destruction. Although, some species can use altered areas, all bats depend on preserved forest at some level [26]. Additionally, neighbouring intact ecosystems serve as diversity insurance for altered areas and allow disturbed areas to regenerate [106]. Long-term sustainability of services will depend on the conservation of structural and functional connectivity between areas. Bats are highly mobile species, but depend on elements such as corridors and stepping-stones for long distance flights. These connectivity structures have been described as essential for the long-term persistence of bats in the Cerrado [48]. Locally, linear connectivity elements can be used to increase landscape heterogeneity of agro-environments and increase bat activity above farms [125-127].

Supporting information

S1 Ecosystem services by bats observed and/or quantified across natural and non-natural systems. (PDF)

S2 Table Pearson correlation between the 19 bioclimatic variables. (PDF)

S3 Table Bioclimatic variables selected and its descriptions (PDF)

S4 Table List of bats known to occur in Brazil and their respective trophic and size attributes. All 182 species were used for the production of size classes. Species in bold (105 in total) are those that produced satisfactory models for potential provision analysis. Column 'Size class' indicates the species sizes: 1= small, 2= medium, 3= large. (PDF)

S5. Graphical representation of proportions of low, medium and high provision potential prior and after deforestation. (PDF)

S6. Structure and results of the two-proportions test assessing differences in the representation of relevant areas for the same service between biomes. (DOC)

S7. Table Proportional losses associated to bats of different size classes (PDF)

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Supplementary information

Table S1. Examples of studies on ecosystem services by bats that observed and/or quantified across natural and non-natural systems. S stands for studies that focused on one species contribution and MS for studies that focused on multiple-species contributions. System points to where the ecosystem services are being delivered. Service estimated value is registered only for services that performed such quantifications and study region and authors are also specified.

Ecosystem Service	Ecosystem service provider (S/MS)	System	Service estimated value (USD)*	Study region	Authors
Pest supression	S (Tadarida brasiliensis)	Cotton plantations	$12.24 millions/yr	United States	López-hoffman et al. 2014
Pest supression	MS (insectivorous)	Cacau agroforestry	$730/ha*yr	Indonesia	Maas et al. 2013
Pest supression	MS (insectivorous)	Coffee agroforestry	-	Mexico	Williams-Guillén et al. 2008
Pest supression	MS (insectivorous)	Corn plantantions	> $1 billion (globally)	United States	Maine and Boyles, 2015
Pest supression	MS (insectivorous)	Macadamia orchads	$57-139/ha/yr	South Africa	Taylor et al. 2017
Seed dispersal and pollination**	MS (frugivorous and nectarivorous)	Cerrado's habitats	-	Brazil	Oliveira et al. 2019
Seed dispersal and pollinatio	MS (frugivorous and nectarivorous)	Ocean islands	-	Fiji	Scanlon et al. 2014
Seed dispersal	MS (frugivorous)	Abandoned pastures	-	Mexico	Gallindo-González et al. 2000
Seed dispersal	MS (frugivorous)	Abandoned pastures	-	Costa Rica	Kelm et al. 2008
Pollination	MS (nectarivorous)	Agave plantations	-	Mexico	Trejo-Salazar et al. 2016
Pollination	MS (nectarivorous)	Durian plantations	$13 millions/yr	Thailand	Bumrungsri et al. 2009

* Quantification of bat species contributions are presented as the original studies.

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Table S1. Results of the Pearson test of correlation between variables. Green cells indicate pairs of highly correlated variables.

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9
bio1	1.0000	-0.3287	0.6518	-0.6784	0.7403	0.9188	-0.6201	0.8328	0.9090
bio10	0.8752	-0.1905	0.2652	-0.2472	0.9185	0.6939	-0.2610	0.8876	0.6617
bio11	0.9628	-0.4132	0.7941	-0.8493	0.5665	0.9645	-0.7724	0.7048	0.9577
bio12	0.4403	-0.4360	0.4709	-0.5373	0.1080	0.5455	-0.5594	0.2219	0.4971
bio13	0.4887	-0.3290	0.6350	-0.6870	0.0806	0.5733	-0.6068	0.2422	0.5739
bio14	0.0184	-0.4388	-0.0634	0.0367	-0.0770	0.1440	-0.2086	-0.0342	0.0272
bio15	0.1289	0.3155	0.3636	-0.3013	0.0249	0.0463	-0.0384	0.0867	0.1665
bio16	0.4952	-0.3359	0.6370	-0.6929	0.0875	0.5805	-0.6111	0.2494	0.5805
bio17	0.0308	-0.4356	-0.0625	0.0344	-0.0630	0.1519	-0.2095	-0.0238	0.0355
bio18	-0.1187	0.0070	-0.2267	0.1105	-0.2184	-0.1752	0.0737	0.0427	-0.2299
bio19	0.3695	-0.5380	0.5094	-0.4093	0.0973	0.5500	-0.5706	0.1255	0.4922
bio2	-0.3287	1.0000	-0.2525	0.4435	0.1543	-0.6137	0.7884	-0.1356	-0.4456
bio3	0.6518	-0.2525	1.0000	-0.9083	0.1646	0.7572	-0.7680	0.3032	0.7962
bio4	-0.6784	0.4435	-0.9083	1.0000	-0.0914	-0.8236	0.8859	-0.3078	-0.8357
bio5	0.7403	0.1543	0.1646	-0.0914	1.0000	0.4803	0.0295	0.7883	0.5145
bio6	0.9188	-0.6137	0.7572	-0.8236	0.4803	1.0000	-0.8626	0.6398	0.9487
bio7	-0.6201	0.7884	-0.7680	0.8859	0.0295	-0.8626	1.0000	-0.2744	-0.7844
bio8	0.8328	-0.1356	0.3032	-0.3078	0.7883	0.6398	-0.2744	1.0000	0.5623
bio9	0.9090	-0.4456	0.7962	-0.8357	0.5145	0.9487	-0.7844	0.5623	1.0000

	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio1	0.9090	0.8752	0.9628	0.4403	0.4887	0.0184	0.1289	0.4952	0.0308	-0.1187	0.3695
bio10	0.6617	1.0000	0.7208	0.2524	0.2019	0.0774	-0.0585	0.2093	0.0919	-0.1236	0.2618
bio11	0.9577	0.7208	1.0000	0.5214	0.6027	0.0148	0.1854	0.6104	0.0246	-0.1378	0.4301
bio12	0.4971	0.2524	0.5214	1.0000	0.8711	0.5987	-0.2787	0.8892	0.6109	0.3730	0.6674
bio13	0.5739	0.2019	0.6027	0.8711	1.0000	0.2112	0.1783	0.9920	0.2181	0.2907	0.5385
bio14	0.0272	0.0774	0.0148	0.5987	0.2112	1.0000	-0.8029	0.2184	0.9930	0.3644	0.5278
bio15	0.1665	-0.0585	0.1854	-0.2787	0.1783	-0.8029	1.0000	0.1573	-0.8186	-0.2233	-0.2781
bio16	0.5805	0.2093	0.6104	0.8892	0.9920	0.2184	0.1573	1.0000	0.2259	0.2917	0.5525
bio17	0.0355	0.0919	0.0246	0.6109	0.2181	0.9930	-0.8186	0.2259	1.0000	0.3713	0.5353
bio18	-0.2299	-0.1236	-0.1378	0.3730	0.2907	0.3644	-0.2233	0.2917	0.3713	1.0000	-0.1714
bio19	0.4922	0.2618	0.4301	0.6674	0.5385	0.5278	-0.2781	0.5525	0.5353	-0.1714	1.0000
bio2	-0.4456	-0.1905	-0.4132	-0.4360	-0.3290	-0.4388	0.3155	-0.3359	-0.4356	0.0070	-0.5380
bio3	0.7962	0.2652	0.7941	0.4709	0.6350	-0.0634	0.3636	0.6370	-0.0625	-0.2267	0.5094
bio4	-0.8357	-0.2472	-0.8493	-0.5373	-0.6870	0.0367	-0.3013	-0.6929	0.0344	0.1105	-0.4093
bio5	0.5145	0.9185	0.5665	0.1080	0.0806	-0.0770	0.0249	0.0875	-0.0630	-0.2184	0.0973
bio6	0.9487	0.6939	0.9645	0.5455	0.5733	0.1440	0.0463	0.5805	0.1519	-0.1752	0.5500
bio7	-0.7844	-0.2610	-0.7724	-0.5594	-0.6068	-0.2086	-0.0384	-0.6111	-0.2095	0.0737	-0.5706
bio8	0.5623	0.8876	0.7048	0.2219	0.2422	-0.0342	0.0867	0.2494	-0.0238	0.0427	0.1255
bio9	1.0000	0.6617	0.9577	0.4971	0.5739	0.0272	0.1665	0.5805	0.0355	-0.2299	0.4922

Table S2. Selected bioclimatic variables selected and its descriptions. These are biologically significant climatic variables and developed by Hijmans et al. (2005) and available at http://worldclim.org/

Bioclimatic variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality
BIO4	Temperature Sasonality
BIO5	Max Temperature of Warmest Month
BIO12	Annual Precipitation
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality

Table S3. List of bats known to occur in Brazil, their respective feeding guild and size classes. All 182 species were used for the production of size classes. Species in bold (105 in total) are those that produced satisfactory models for potential provision analysis. Column 'Size class' indicates the species sizes: 1=small, 2=medium, 3=large.

Family	Species	Trophic Id	FA (mm)	Size class
Emballonuridae				
	Centronycteris_maximiliani	In	45.0	2
	Cormura_brevirostris	In	46.5	2
	Cyttarops_alecto	In	47	2
	Diclidurus ingens	In	71.5	3
	Diclidurus isabella	In	59.3	3
	Diclidurus_albus	In	66	3
	Diclidurus_scutatus	In	54.2	2
	Peropteryx_kappleri	In	46	2
	Peropteryx_leucoptera	In	45	2
	Peropteryx_macrotis	In	38.3	1
	Peropteryx_pallidoptera	In	41	1
	Peropteryx_trinitatis	In	39	1
	Rhynchonycteris_naso	In	37	1
	Saccopteryx_bilineata	In	46	2
	Saccopteryx_canescens	In	38	1
	Saccopteryx_gymnura	In	34	1
	Saccopteryx_leptura	In	41	1
Furipteridae				
	Furipterus_horrens	In	35.5	1
Molossidae				
	Cynomops_abrasus	In	45	2
	Cynomops_greenhalli	In	36	1
	Cynomops_mastivus	In	43	2
	Cynomops_milleri	In	31.5	1
	Cynomops_planirostris	In	30.5	1
	Eumops_auripendulus	In	61	3
	Eumops_bonariensis	In	48	2
	Eumops_chimaera	In	67.25	3
	Eumops_dabbenei	In	76.5	3
	Eumops_delticus	In	47.6	2
	Eumops_glaucinus	In	60.5	3
	Eumops_hansae	In	39	1
	Eumops_maurus	In	52	2
	Eumops_patagonicus	In	54.5	2
	Eumops_perotis	In	76.5	3
	Eumops_trumbulli	In	66.5	3
	Molossops_neglectus	In	35.5	1
	Molossops_temminckii	In	28.5	1

Family	Species	Trophic Id	FA (mm)	Size class
	Molossus_aztecus	In	38	1
	Molossus_coibensis	In	35	1
	Molossus_currentium	In	41.5	1
	Molossus_molossus	In	41.5	1
	Molossus_pretiosus	In	45	2
	Molossus_rufus	In	50	2
	Neoplatymops_mattogrossensis	In	30	1
	Nyctinomops_aurispinosus	In	50.5	2
	Nyctinomops_laticaudatus	In	44	2
	Nyctinomops_macrotis	In	58.2	3
	Promops_centralis	In	54	2
	Promops_nasutus	In	48	2
	Tadarida_brasiliensis	In	42.5	1
Mormoopidae				
	Pteronotus_alitonus	In	61.65	3
	Pteronotus_gymnonotus	In	52.5	2
	Pteronotus_personatus	In	44	1
	Pteronotus_rubiginosus	In	63.9	3
Natalidae				
	Natalus_macrourus	In	38	1
Noctilionidae				
	Noctilio_albiventris	Ps/Is	62	1 / 3
	Noctilio_leporinus	Ps/Is	80	2 / 3
Phyllostomidae				
	Ametrida_centurio	Fr	28.5	1
	Anoura_caudifer	Nec	35.29	1
	Anoura_geoffroyi	Nec	40.3	3
	Artibeus_concolor	Fr	47.5	2
	Artibeus_fimbriatus	Fr	63.98	3
	Artibeus_lituratus	Fr	71.5	3
	Artibeus_obscurus	Fr	64	3
	Artibeus_planirostris	Fr	64.5	3
	Carollia_benkeithi	Fr	36.5	1
	Carollia_brevicauda	Fr	34.5	1
	Carollia_perspicillata	Fr	41	1
	Chiroderma_doriae	Fr	52.5	2
	Chiroderma_trinitatum	Fr	36.4	1
	Chiroderma_villosum	Fr	47	2
	Chiroderma_vizottoi	Fr	48.5	2
	Choeroniscus_minor	Nec	32.5	1
	Chrotopterus_auritus	Ca	82	2
	Dermanura_anderseni	Fr	39	1
	Dermanura_bogotensis	Fr	35	1
	Dermanura_cinerea	Fr	38	1

Family	Species	Trophic Id	FA (mm)	Size class
	Dermanura_gnoma	Fr	38	1
	Desmodus_rotundus	He	57.5	
	Diaemus_youngi	He	53	
	Diphylla_ecaudata	He	56	
	Dryadonycteris_capixaba	Nec	30.7	1
	Gardnerycteris_crenulatum	In	48	2
	Glossophaga_commissarisi	Nec	34.5	1
	Glossophaga_longirostris	Nec	38.5	2
	Glossophaga_soricina	Nec/Fr/ In	35.5	1 / 1 / 1
	Glyphonycteris_behnii	In	47	2
	Glyphonycteris_daviesi	In/Fr	55.5	2 / 3
	Glyphonycteris_sylvestris	In	40.5	1
	Hsunycteris_pattoni	Nec	32	1
	Hsunycteris_thomasi	Nec	32.5	1
	Lampronycteris_brachyotis	In	41	1
	Lichonycteris_degener	Nec	33	1
	Lionycteris_spurrelli	Nec	35	1
	Lonchophylla_bokermanni	Nec	38.5	2
	Lonchophylla_dekeyseri	Nec	36.9	2
	*Lonchophylla_inexpectata**	Nec	34.15	1
	Lonchophylla_mordax	Nec	33.9	1
	Lonchophylla_peracchii	Nec	35.45	1
	Lonchorhina_aurita	In	50.5	2
	Lonchorhina_inusitata	In	54.5	2
	Lophostoma_brasiliense	In	34	1
	Lophostoma_schulzi	In	44	2
	Lophostoma_silvicola	In	54.5	2
	Macrophyllum_macrophyllum	In	36	1
	Mesophylla_macconnelli	Fr	31.5	1
	Micronycteris_hirsuta	In	43	1
	Micronycteris_homezorum	In	35.5	1
	Micronycteris_megalotis	In	34	1
	Micronycteris_microtis	In	34.5	1
	Micronycteris_minuta	In	34	1
	Micronycteris_sanborni	In	34	1
	Micronycteris_schmidtorum	In	35.5	1
	Mimon_bennettii	In	55	2
	Phylloderma_stenops	In	74	3
	Phyllostomus_discolor	In	62	3
	Phyllostomus_elongatus	In	66	3
	Phyllostomus_hastatus	Ca	85	2
	Phyllostomus_latifolius	In	58.5	3
	Platyrrhinus_angustirostris	Fr	37.5	1
	Platyrrhinus_aurarius	Fr	52.5	2

Family	Species	Trophic Id	FA (mm)	Size class
	Platyrrhinus_brachycephalus	Fr	37.5	1
	Platyrrhinus_brachycephalus	Fr	37.5	1
	Platyrrhinus_fusciventris	Fr	37.5	1
	Platyrrhinus_incarum	Fr	37.5	1
	Platyrrhinus_infuscus	Fr	58	3
	Platyrrhinus_lineatus	Fr	47.5	2
	*Platyrrhinus_recifinus**	Fr	42.9	2
	Pygoderma_bilabiatum	Fr	40	1
	Rhinophylla_fischerae	Fr	31.5	1
	Rhinophylla_pumilio	Fr	34.5	1
	Scleronycteris_ega	Nec	34	1
	Sphaeronycteris_toxophyllum	Fr	39.5	1
	Sturnira_lilium	Fr	40.5	1
	Sturnira_magna	Fr	57.5	3
	Sturnira_tildae	Fr	46	2
	Tonatia_bidens	In	54	2
	Tonatia_saurophila	In	55	2
	Trachops_cirrhosus	Ca	61.5	1
	Trinycteris_nicefori	In	41	1
	Uroderma_bilobatum	Fr	42	2
	Uroderma_magnirostrum	Fr	42	2
	Vampyressa_pusilla	Fr	33	1
	Vampyressa_thyone	Fr	33	1
	Vampyriscus_bidens	Fr	36	1
	Vampyriscus_brocki	Fr	32	1
	Vampyrodes_caraccioli	Fr	51.5	2
	Vampyrum_spectrum	Ca	101	3
	Xeronycteris_vieirai	Nec	37.15	2
	Lophostoma_carrikeri	In	46	2
Thyropteridae				
	Neonycteris_pusilla	In	34	1
	Thyroptera_devivoi	In	36.5	1
	Thyroptera_discifera	In	33.5	1
	Thyroptera_lavali	In	39	1
	Thyroptera_tricolor	In	36.5	1
	Thyroptera_wynneae	In	34	1
Vespertilioninae				
	Eptesicus_andinus	In	40.5	1
	Eptesicus_brasiliensis	In	43	2
	Eptesicus_chiriquinus	In	45.5	2
	Eptesicus_diminutus	In	39.5	1
	Eptesicus_furinalis	In	39	1
	*Eptesicus_taddeii**	In	46.5	2
	Histiotus_alienus	In	45.75	2

Family	Species	Trophic Id	FA (mm)	Size class
	Histiotus_diaphanopterus	In	45.35	2
	Histiotus_laephotis	In	46.9	2
	Histiotus_montanus	In	47.7	2
	Histiotus_velatus	In	46	2
	Lasiurus_blossevillii	In	39.5	1
	Lasiurus_castaneus	In	45	2
	Lasiurus_cinereus	In	53.5	2
	Lasiurus_ebenus	In	45.7	2
	Lasiurus_ega	In	46	2
	Lasiurus_egregius	In	49	2
	Lasiurus_salinae	In		NA
	Myotis_albescens	In	34	1
	Myotis_izecksohni	In	37.4	1
	Myotis_lavali	In	34	1
	Myotis_levis	In	40.775	1
	Myotis_nigricans	In	34	1
	Myotis_riparius	In	34.5	1
	Myotis_ruber	In	39.99	1
	Myotis_simus	In	38.5	1
	Rhogeessa_hussoni	In	29.5	1
	Rhogeessa_io	In	30	1

Observation: In = Insectivorous

Fr = Frugivorous

Nec = Nectarivorous

Ca = Carnivorous

Ps = Piscivory (included as carnivorous)

1. ALL BATS
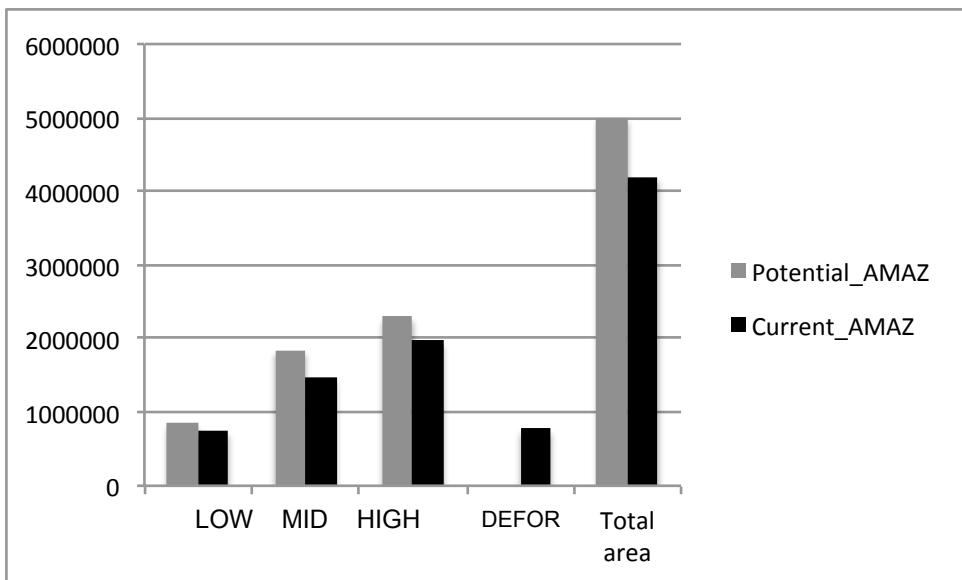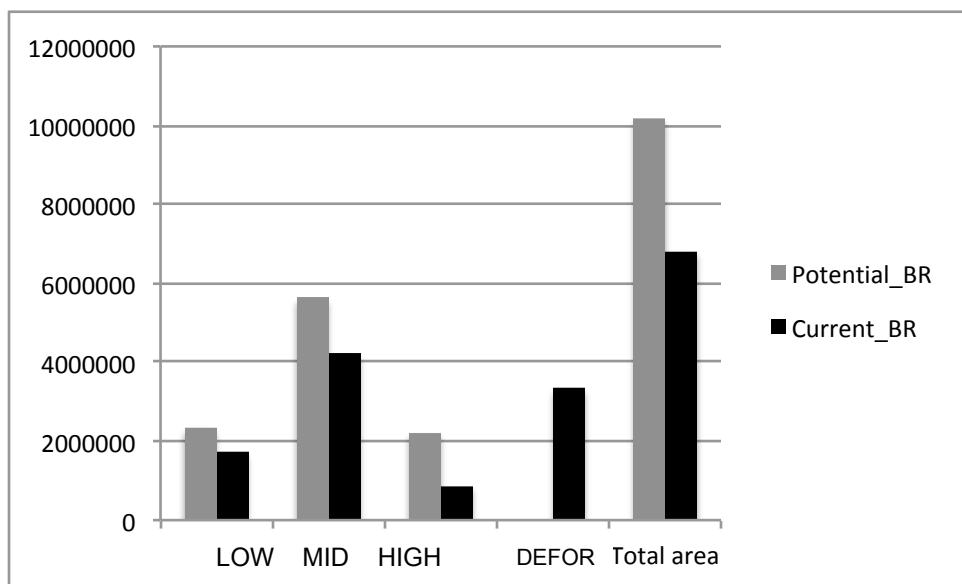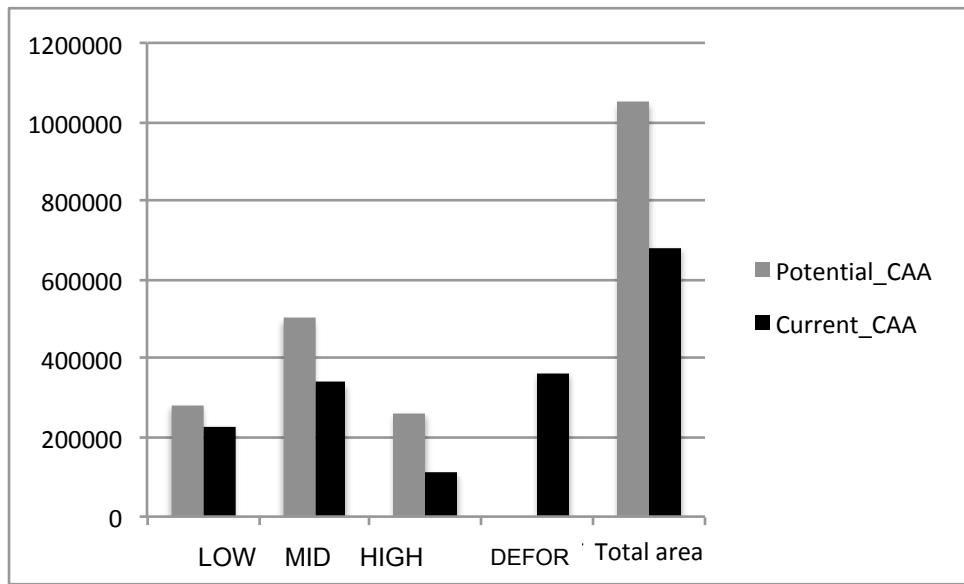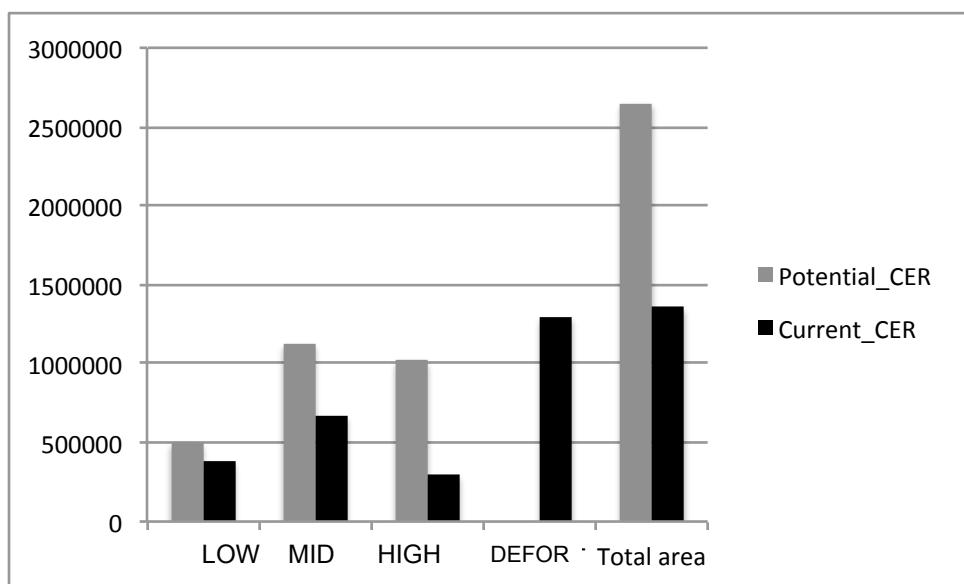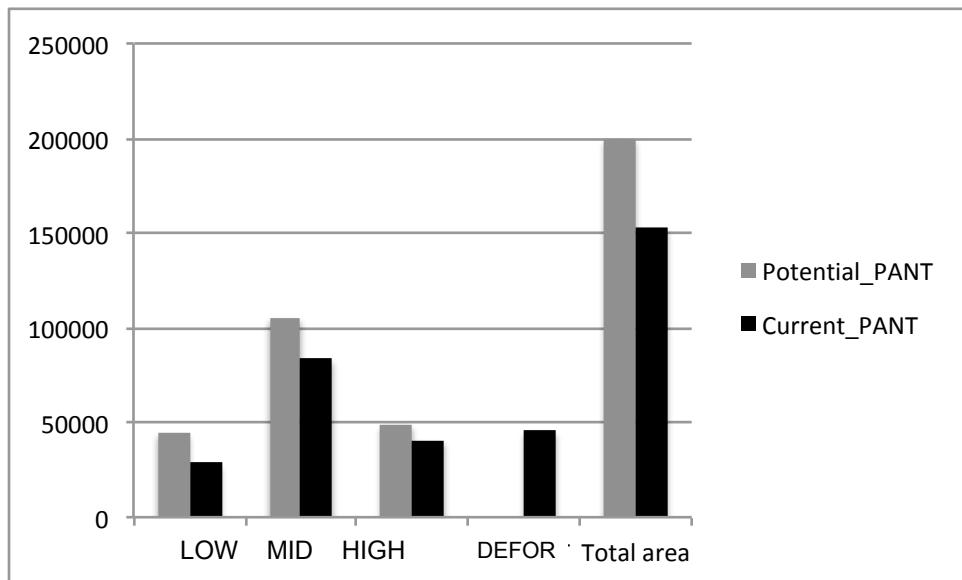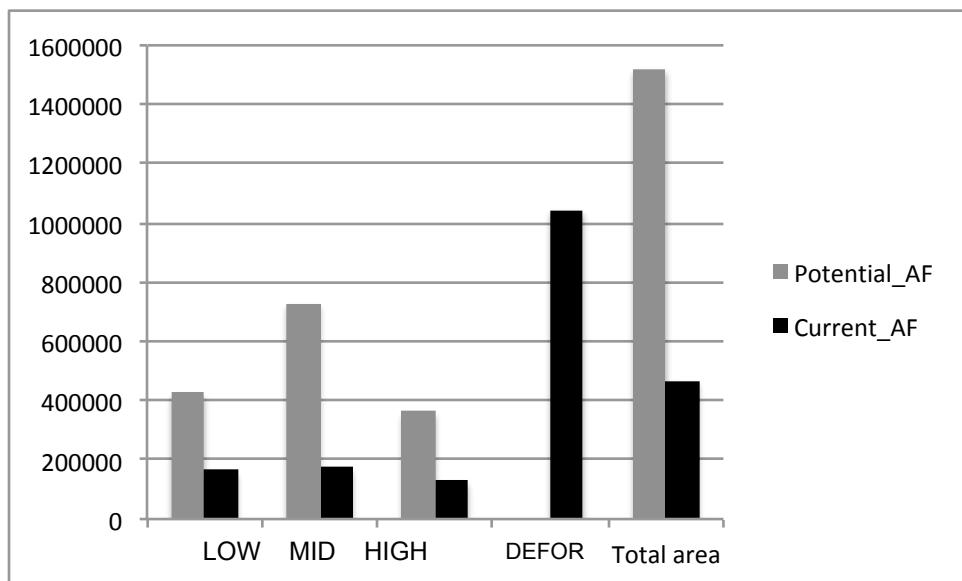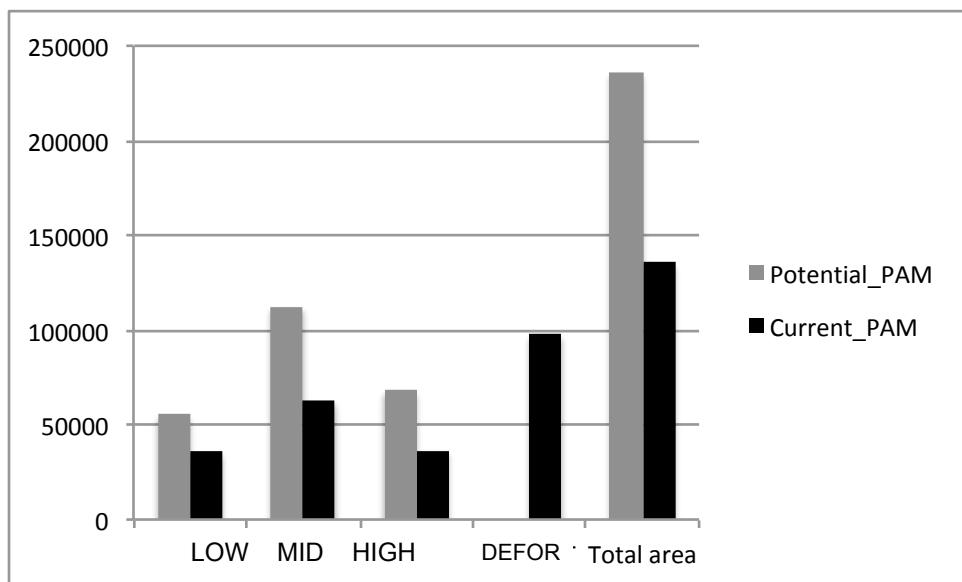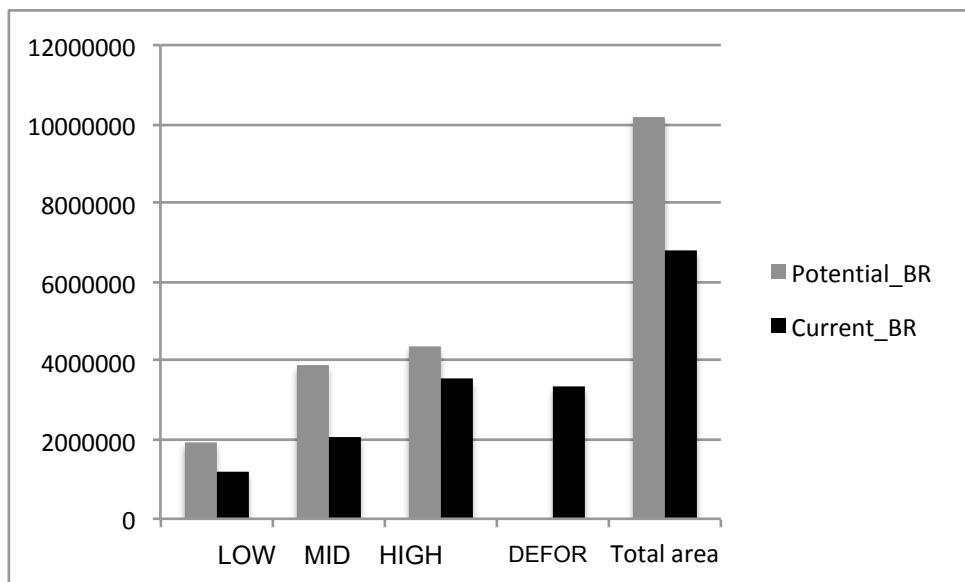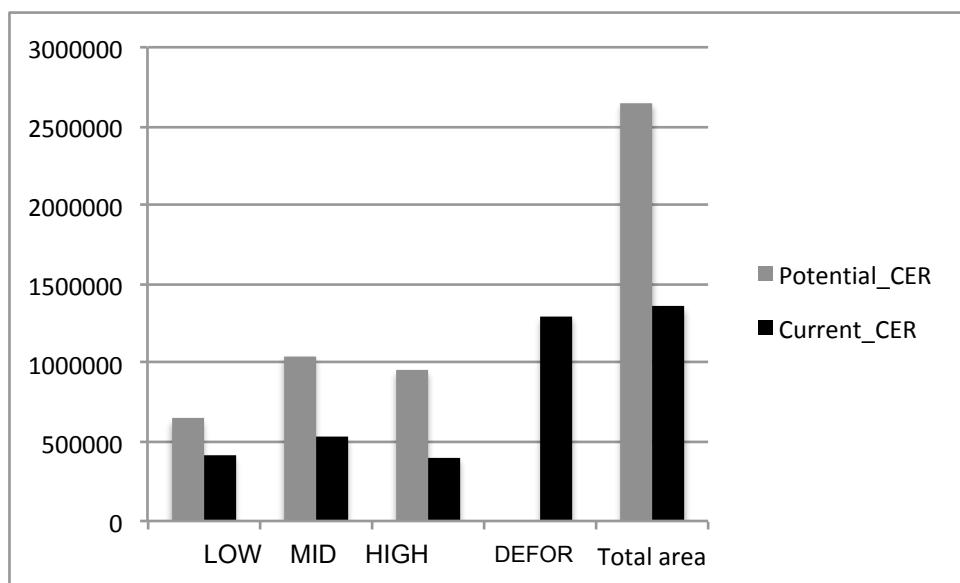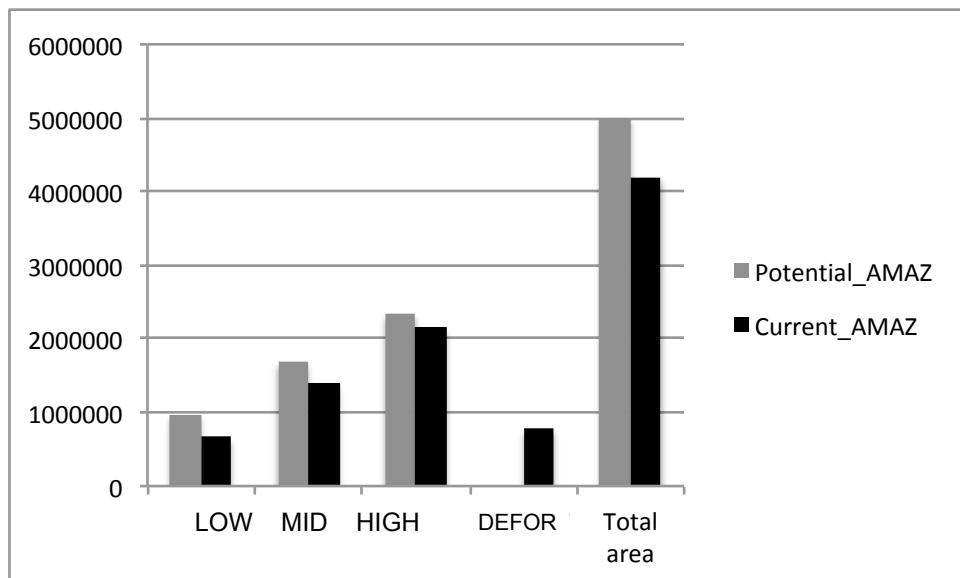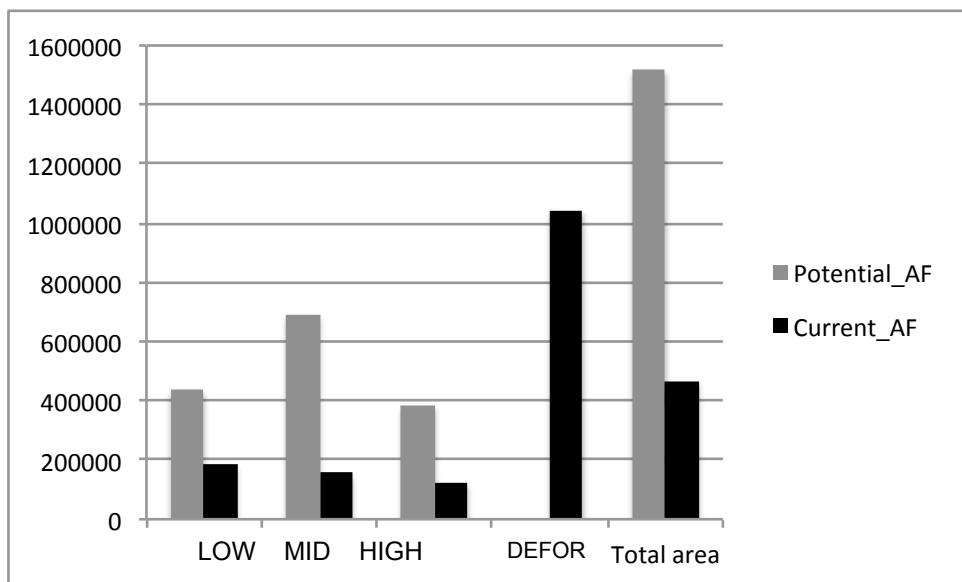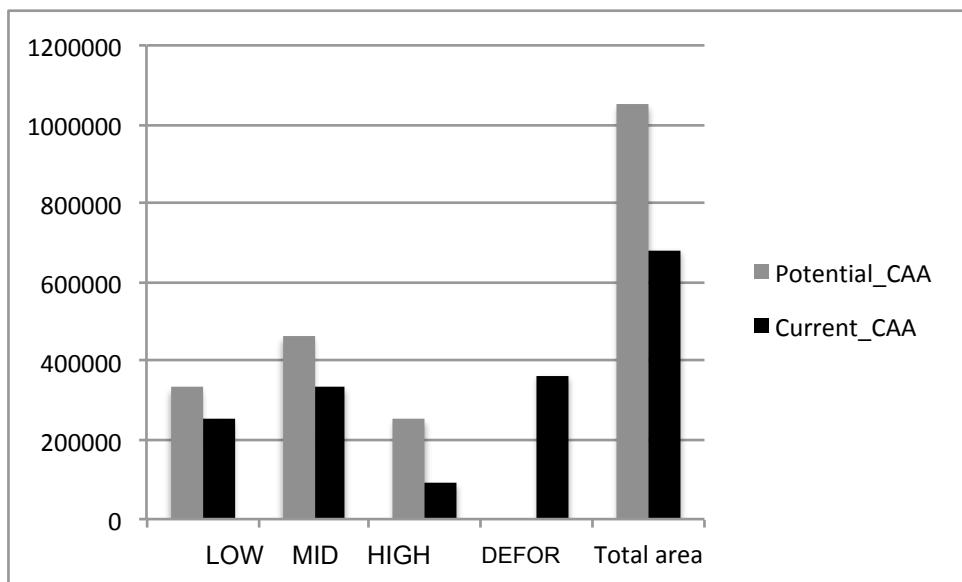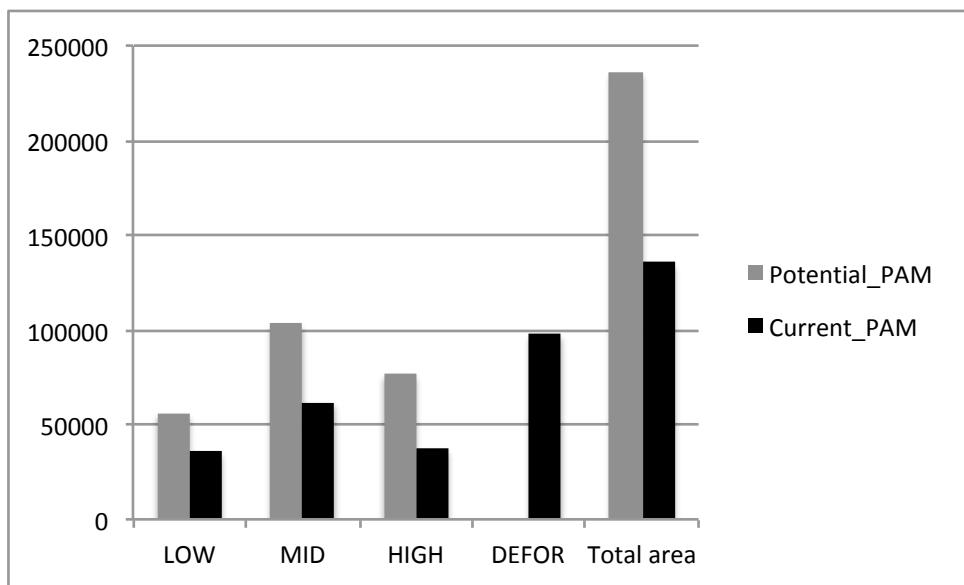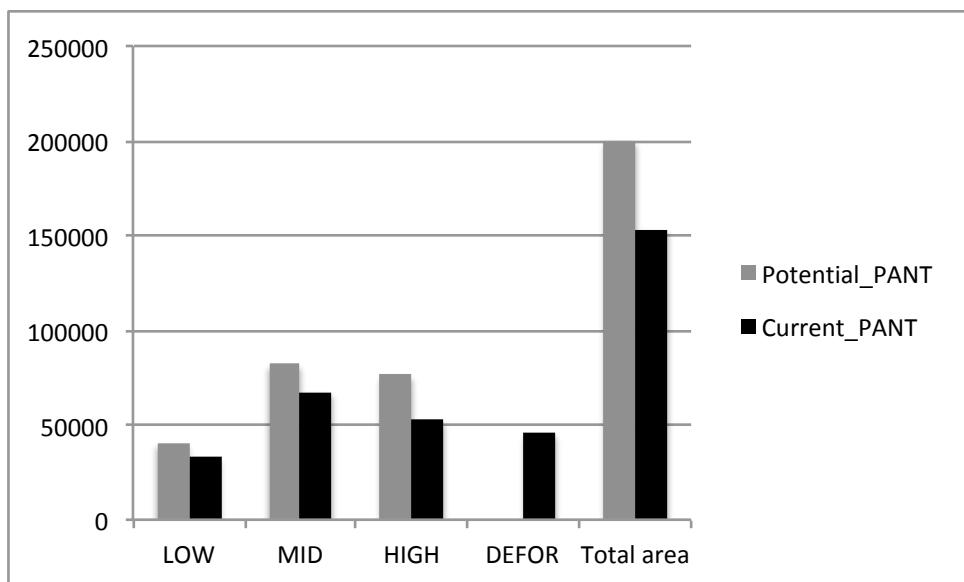
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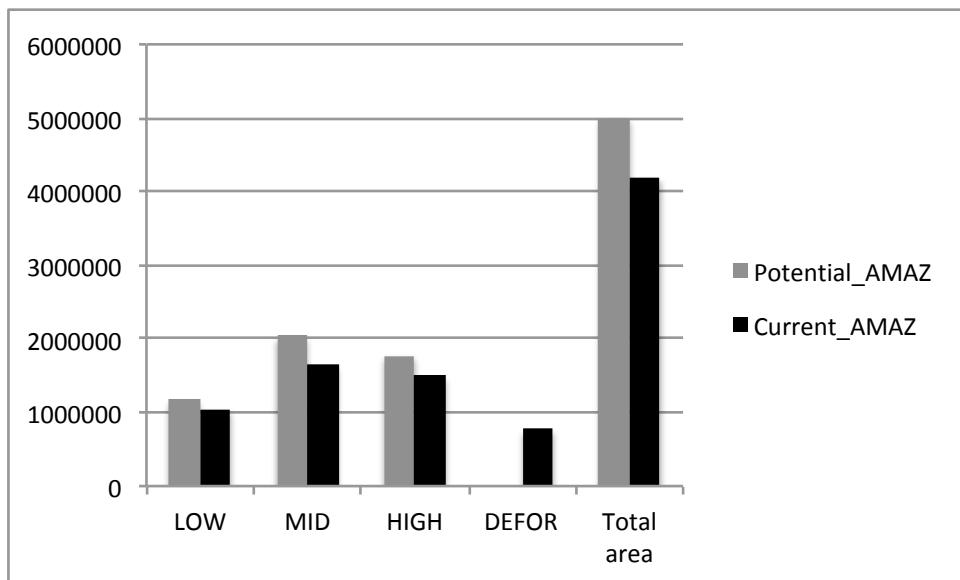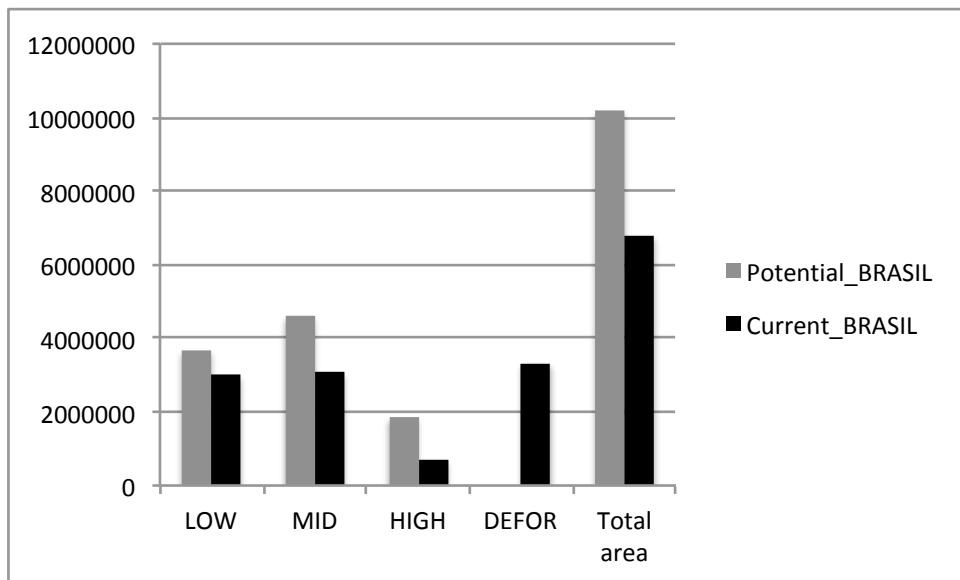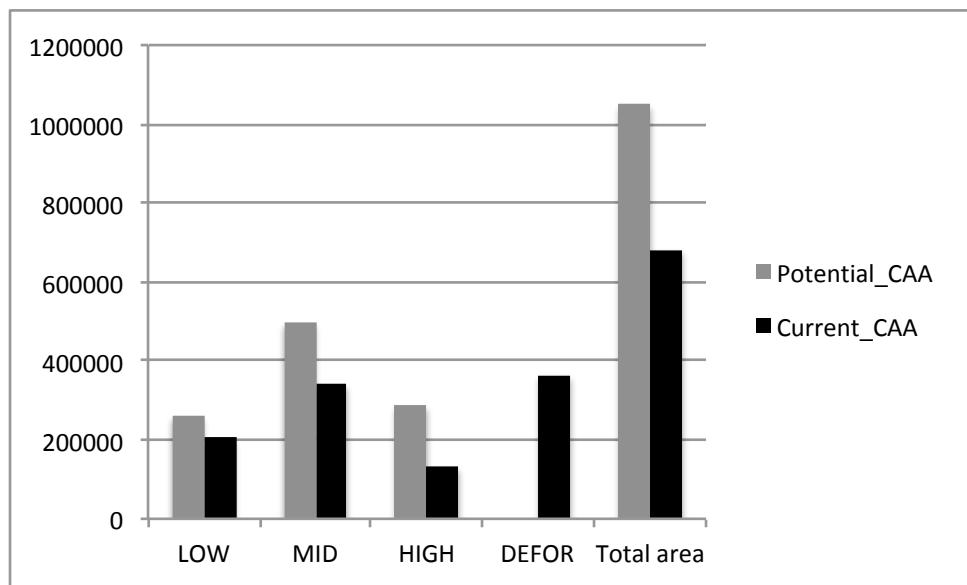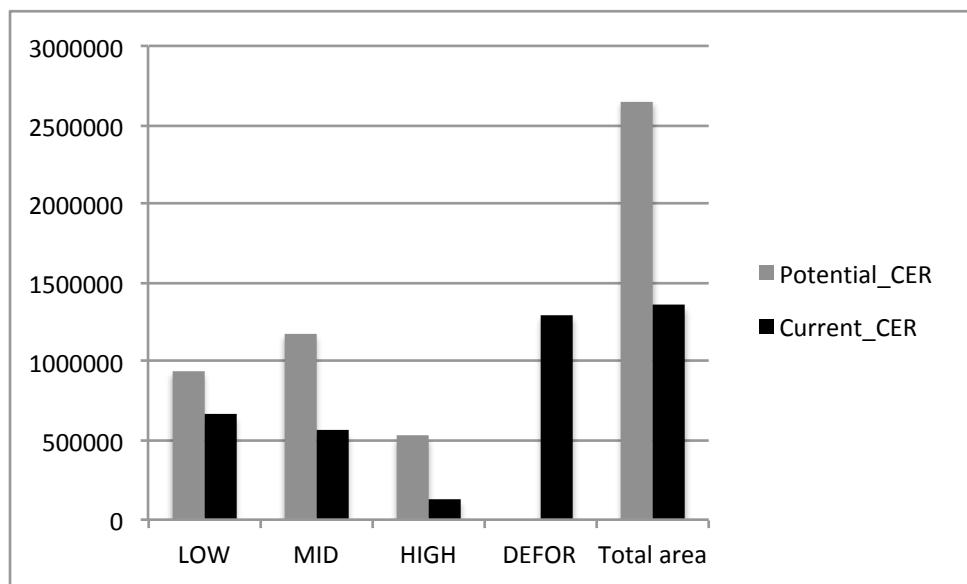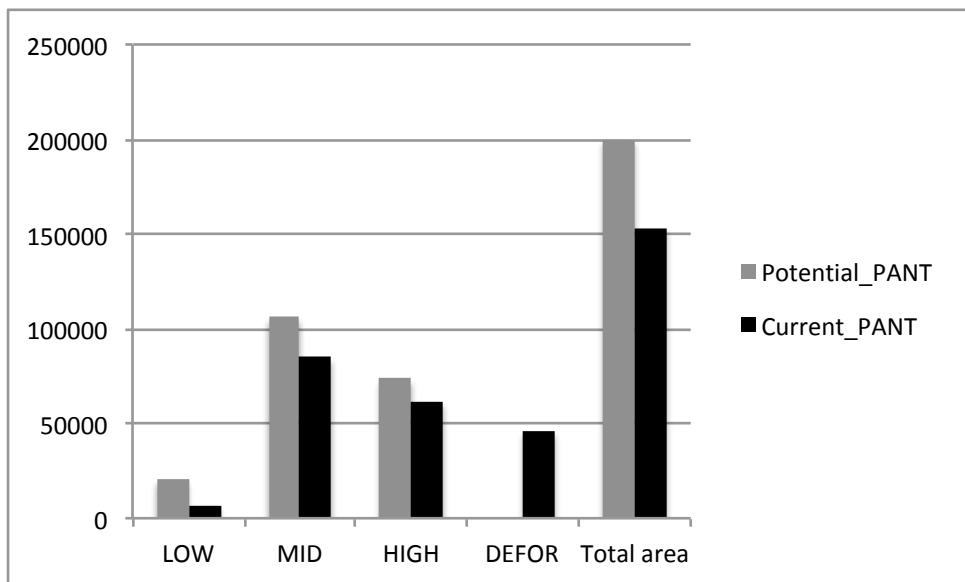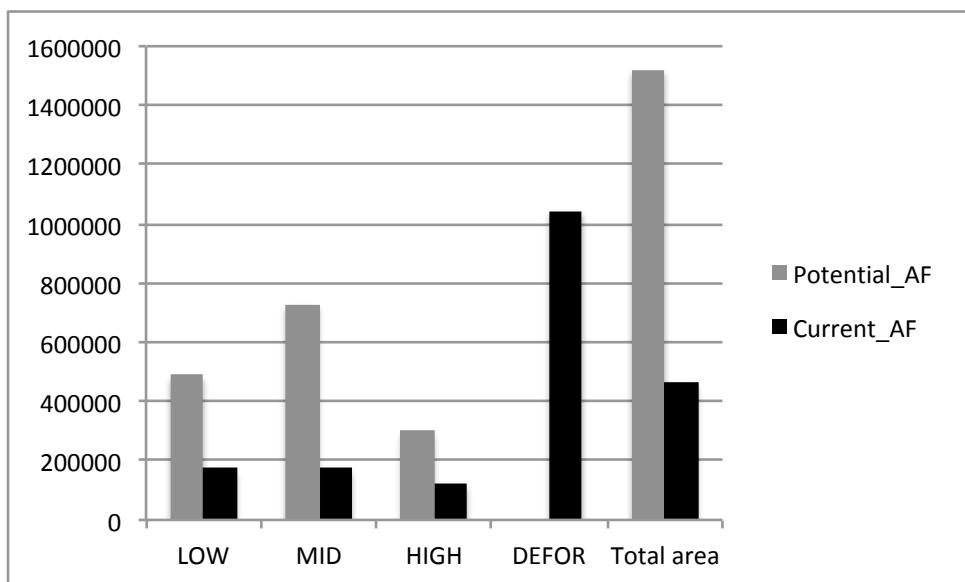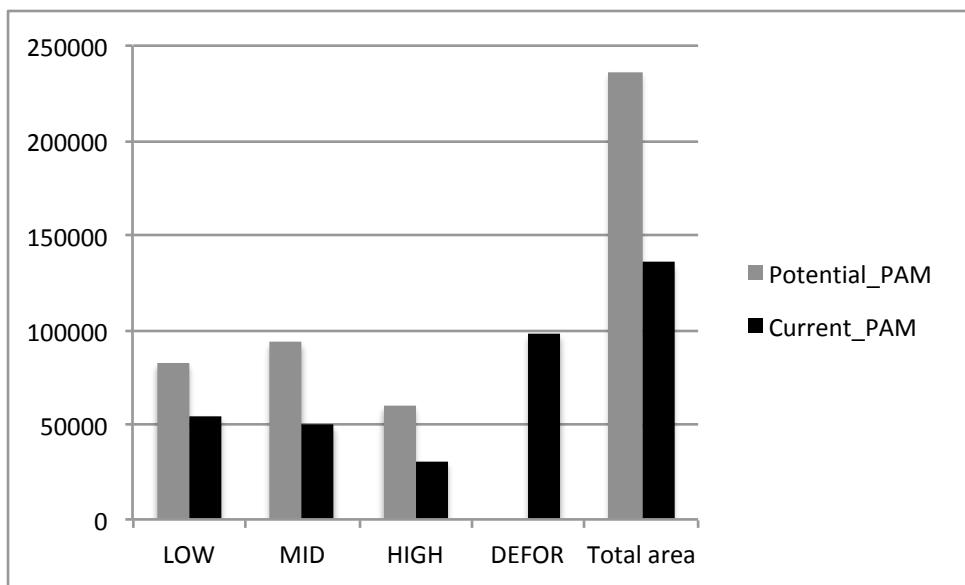
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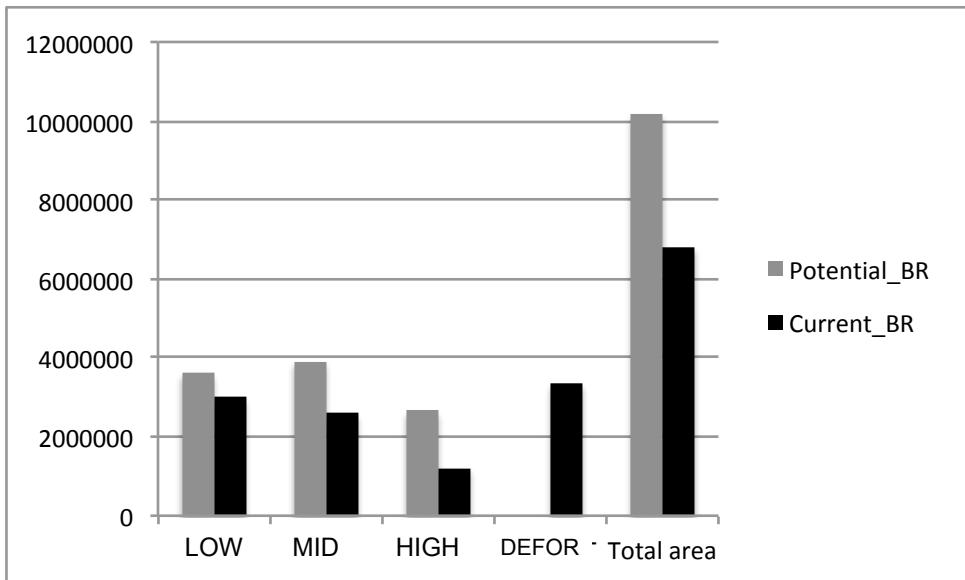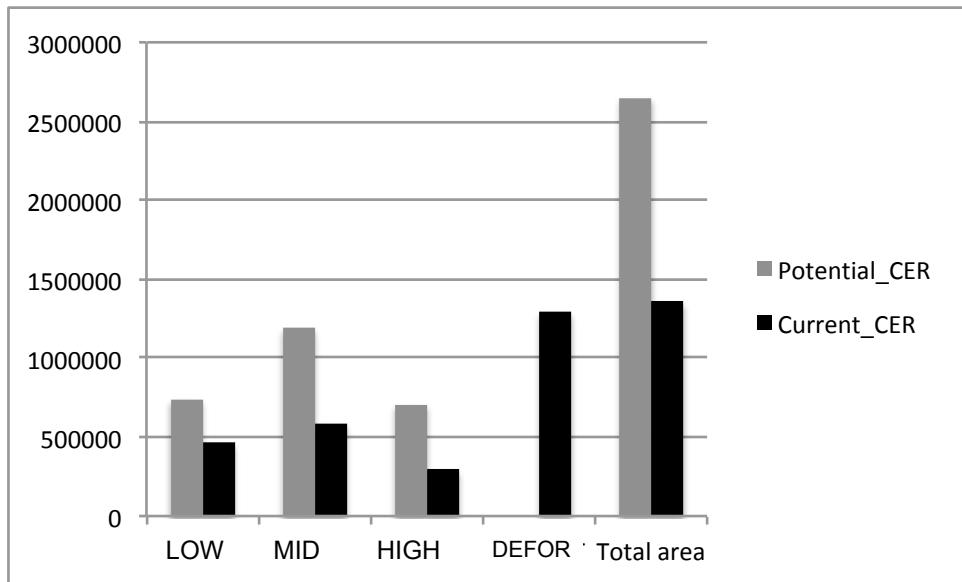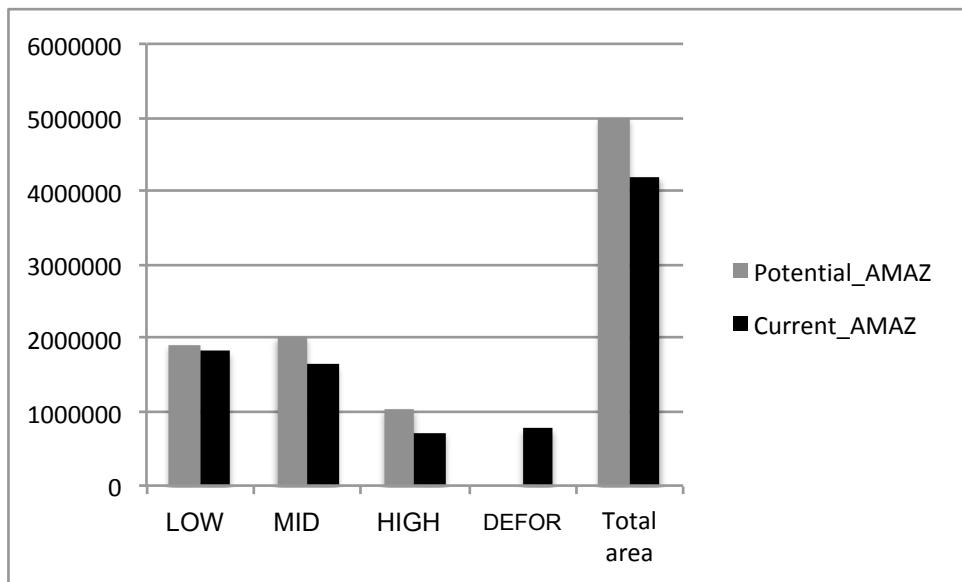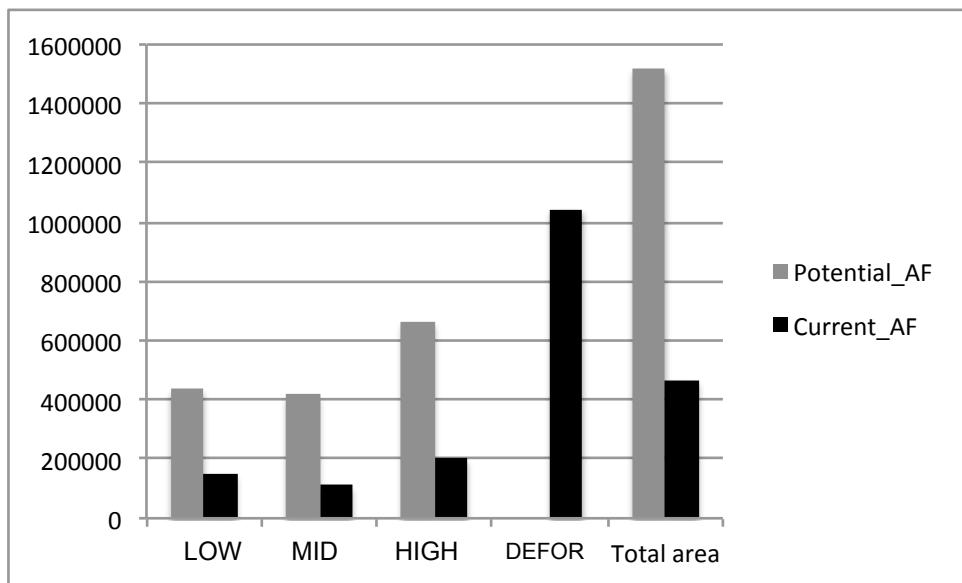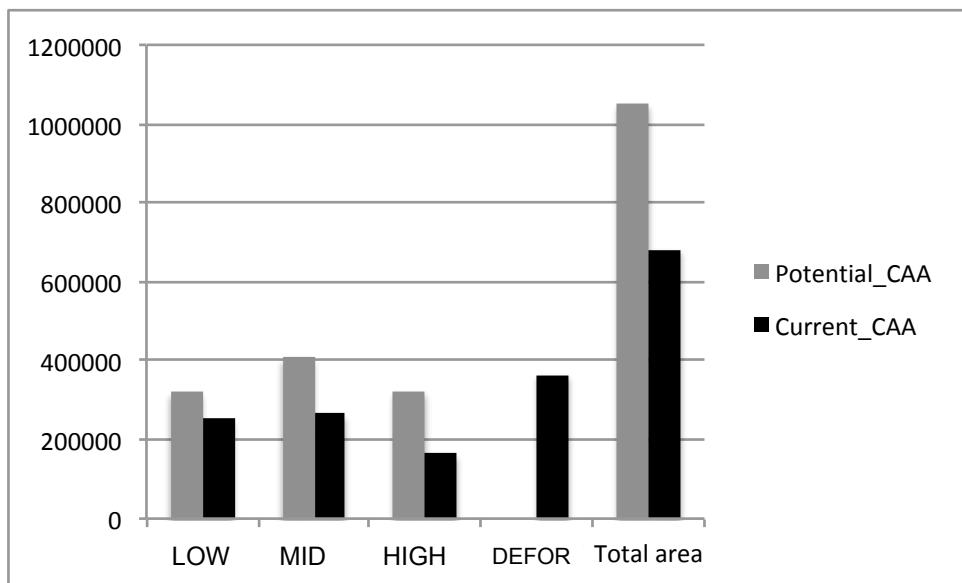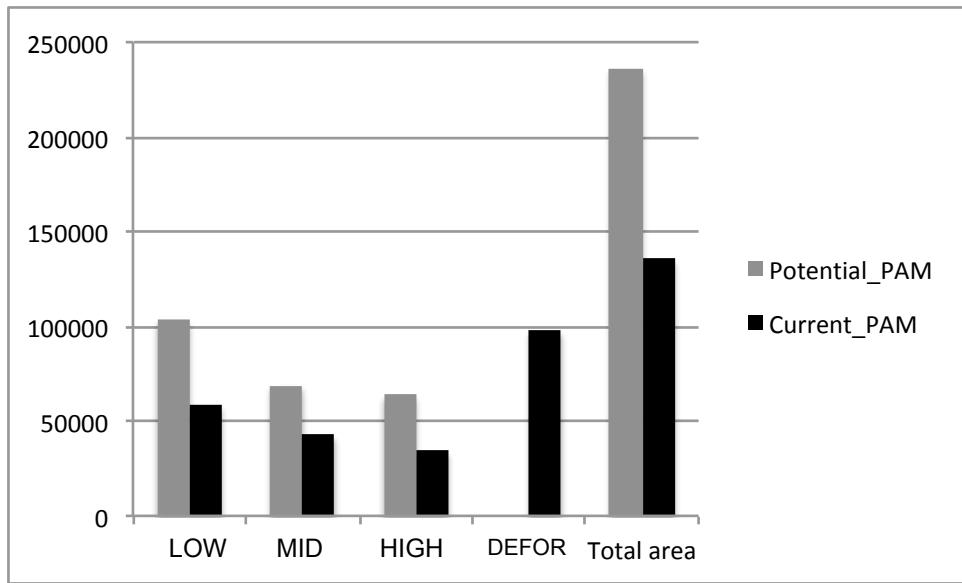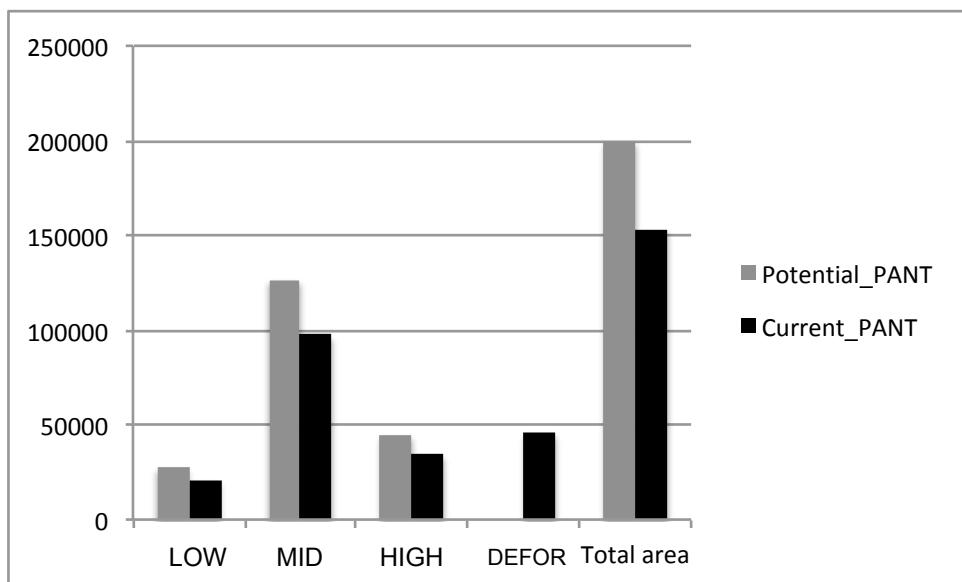
5. CARNIVORY
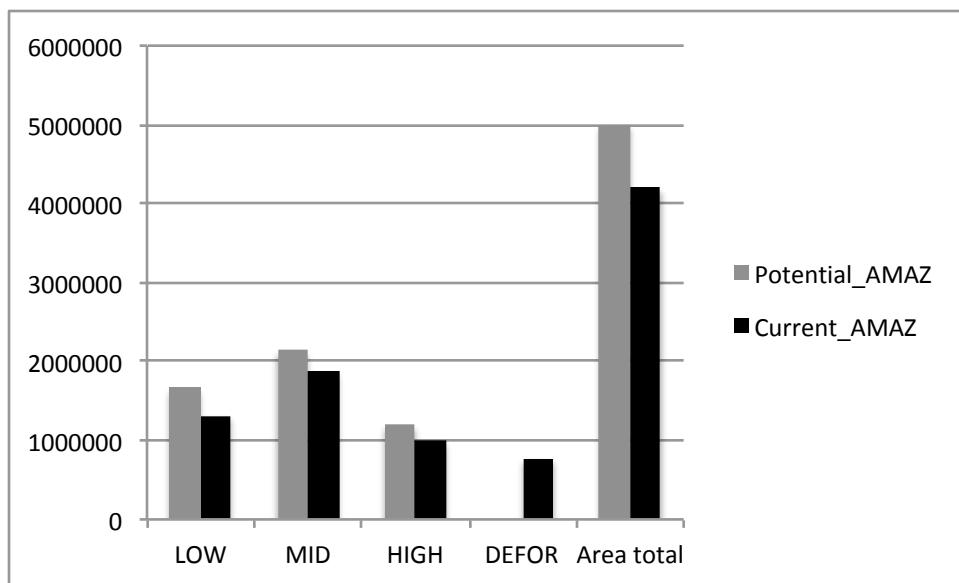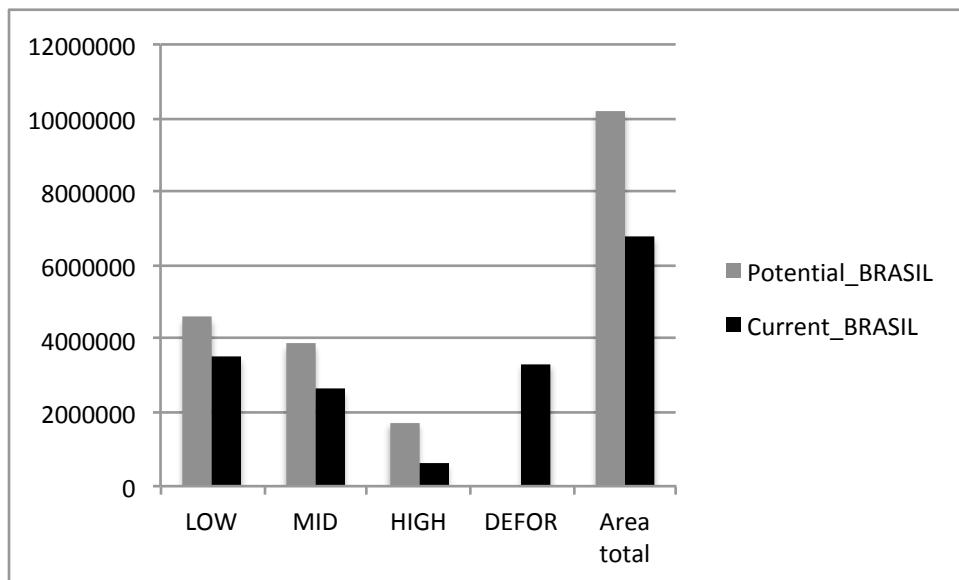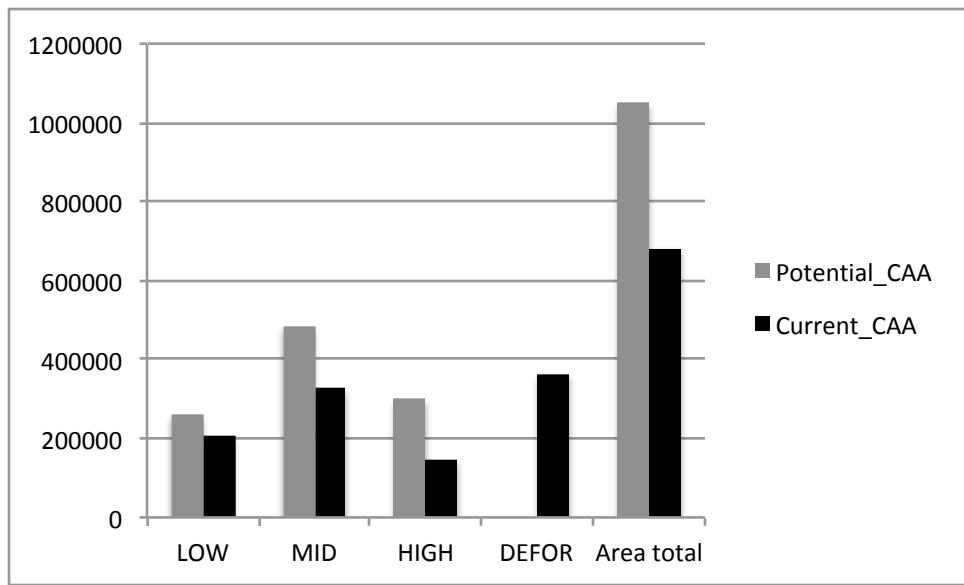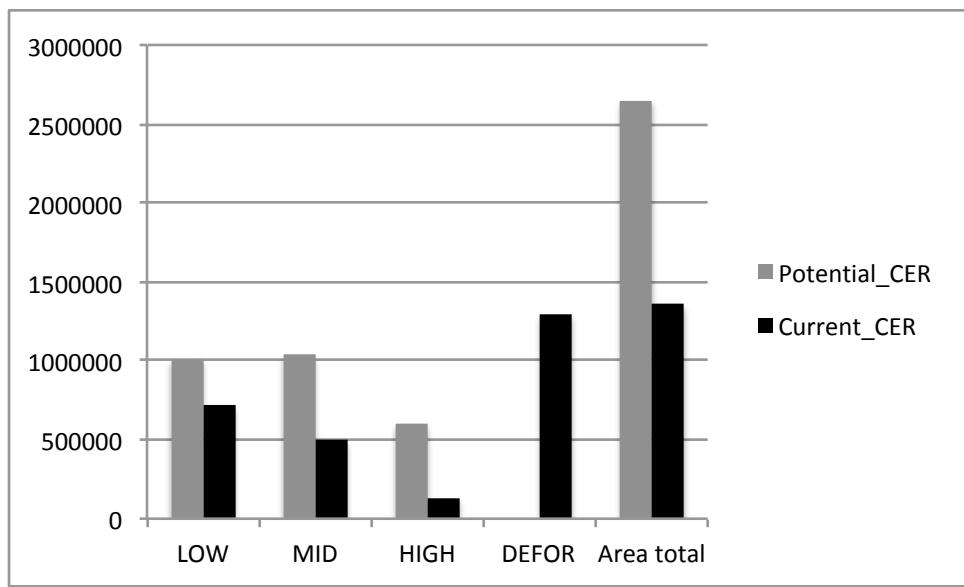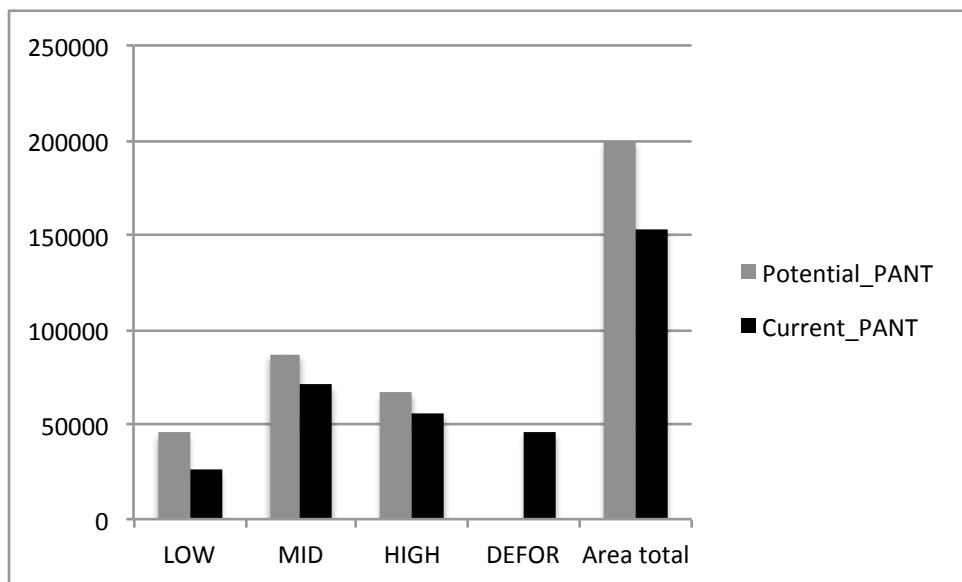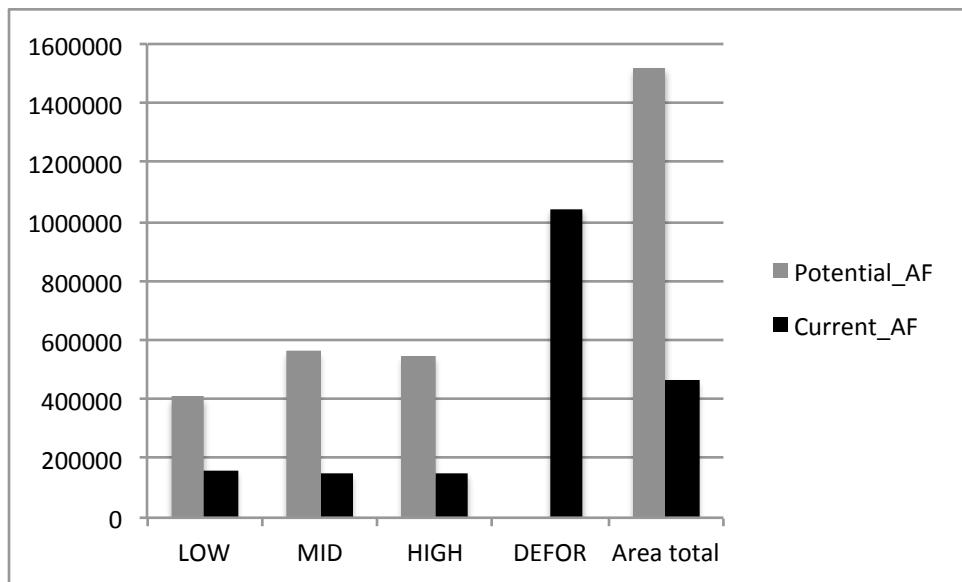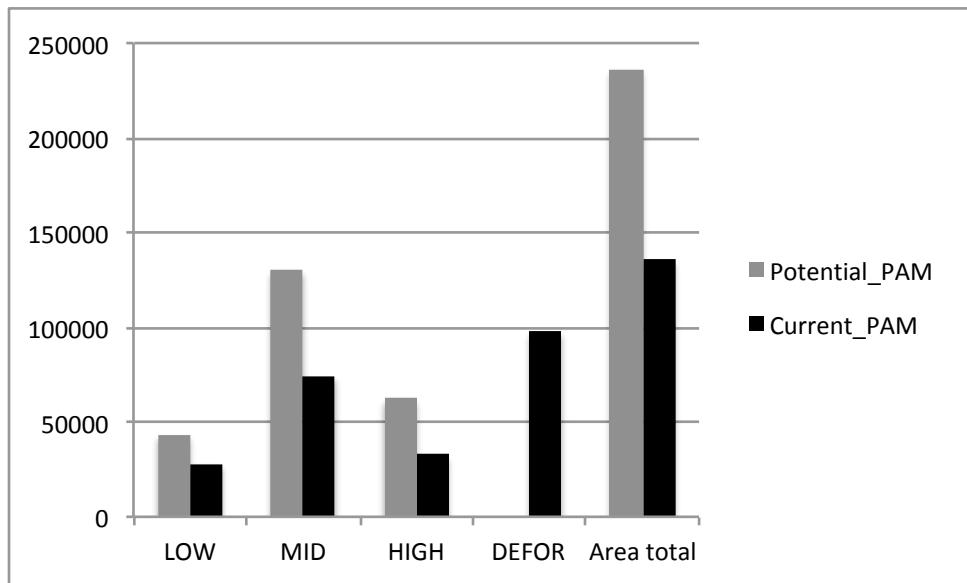
S4. Structure and results of the two-proportions test assessing differences in the representation of relevant areas for the same service between biomes

FRUGIVORY

Amazon vs Cerrado
prop.test(c(4019602, 2004915), c(4993375, 2650258))
X-squared = 24382, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.804987 0.756498

Amazon vs Caatinga
prop.test(c(4019602, 716698), c(4993375, 1049346))
X-squared = 76152, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8049870 0.6829949

Amazon vs Atlantic forest
prop.test(c(4019602, 1078623), c(4993375, 1517823))
X-squared = 60981, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8049870 0.7106382

Amazon vs Pantanal
prop.test(c(4019602, 158836), c(4993375, 199688))
X-squared = 111.71, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8049870 0.7954209

Amazon vs Pampa
prop.test(c(4019602, 179884), c(4993375, 235992))
X-squared = 2602.5, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8049870 0.7622462

Cerrado vs Caatinga
prop.test(c(2004915, 716698), c(2650258, 1049346))
X-squared = 20884, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7564980 0.6829949

Cerrado vs Atlantic forest
prop.test(c(2004915, 1078623), c(2650258, 1517823))
X-squared = 10544, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7564980 0.7106382

Cerrado vs Pantanal
prop.test(c(2004915, 158836), c(2650258, 199688))
X-squared = 1538.8, df = 1, p-value < 2.2e-16
 prop 1   prop 2

0.7564980 0.7954209

Cerrado vs Pampa
prop.test(c(2004915, 179884), c(2650258, 235992))
X-squared = 38.888, df = 1, p-value = 4.488e-10
 prop 1   prop 2
 0.7564980 0.7622462

Caatinga vs Atlantic forest
prop.test(c(716698, 1078623), c(1049346, 1517823))
X-squared = 2254.6, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6829949 0.7106382

Caatinga vs Pantanal
prop.test(c(716698, 158836), c(1049346, 199688))
X-squared = 10116, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6829949 0.7954209

Caatinga vs Pampa
prop.test(c(716698, 179884), c(1049346, 235992))
X-squared = 5735.2, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6829949 0.7622462

Atlantic forest vs Pantanal
prop.test(c(1078623, 158836), c(1517823, 199688))
X-squared = 6298.5, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.7106382 0.7954209

Atlantic forest vs Pampa
prop.test(c(1078623, 179884), c(1517823, 235992))
X-squared = 2683.9, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.7106382 0.7622462

Pantanal vs Pampa
prop.test(c(158836, 179884), c(199688, 235992))
X-squared = 687.82, df = 1, p-value < 2.2e-16
 prop 1   prop 2
0.7954209 0.7622462

Conclusion: Provision potential of ecosystem services related to frugivory is differentially represented across Brazil.

INSECTIVORY
Amazon vs Cerrado
prop.test(c(3816478, 1707230), c(4993375, 2650258))

X-squared = 124670, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7643083 0.6441750

Amazon vs Caatinga
prop.test(c(3816478, 787458), c(4993375, 1049345))
X-squared = 920.82, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.7643083 0.7504281

Amazon vs Atlantic forest
prop.test(c(3816478, 1029058), c(4993375, 1517823))
X-squared = 45564, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.7643083 0.6779829

Amazon vs Pantanal
prop.test(c(3816478, 179295), c(4993375, 199688))
X-squared = 19309, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7643083 0.8978757

Amazon vs Pampa
prop.test(c(3816478, 153366), c(4993375, 236001))
X-squared = 16145, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7643083 0.6498532

Cerrado vs Caatinga
prop.test(c(1707230, 787458), c(2650258, 1049345))
X-squared = 38643, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6441750 0.7504281

Cerrado vs Atlantic forest
prop.test(c(1707230, 1029058), c(2650258, 1517823))
X-squared = 4891.3, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6441750 0.6779829

Cerrado vs Pantanal
prop.test(c(1707230, 179295), c(2650258, 199688))
X-squared = 53411, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6441750 0.8978757

Cerrado vs Pampa
prop.test(c(1707230, 153366), c(2650258, 236001))
X-squared = 30.475, df = 1, p-value = 3.382e-08
 prop 1   prop 2

0.6441750 0.6498532

Caatinga vs Atlantic forest
prop.test(c(787458, 1029058), c(1049345, 1517823))
X-squared = 15737, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.7504281 0.6779829

Caatinga vs Pantanal
prop.test(c(787458, 179295), c(1049345, 199688))
X-squared = 30.475, df = 1, p-value = 3.382e-08
 prop 1   prop 2
 0.6441750 0.6498532

Caatinga vs Pampa
prop.test(c(787458, 153366), c(1049345, 236001))
X-squared = 9933.1, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7504281 0.6498532

Atlantic forest vs Pantanal
prop.test(c(1029058, 179295), c(1517823, 199688))
X-squared = 40911, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6779829 0.8978757

Atlantic forest vs Pampa
prop.test(c(1029058, 153366), c(1517823, 236001))
X-squared = 735.63, df = 1, p-value < 2.2e-16
 prop 1   prop 2
0.6779829 0.6498532

Pantanal vs Pampa
prop.test(c(179295, 153366), c(199688, 236001))
X-squared = 36851, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8978757 0.6498532

Conclusion: Provision potential of ecosystem services related to insectivory is differentially represented across Brazil.

NECTARIVORY
Amazon vs Cerrado
prop.test(c(3074476, 1906416), c(4993368, 2650259))
X-squared = 81890, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6157119 0.7193320

Amazon vs Caatinga
prop.test(c(3074476, 729425), c(4993368, 1049346))

X-squared = 23445, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6157119 0.6951234

Amazon vs Atlantic forest
prop.test(c(3074476, 1081309), c(4993368, 1517823))
X-squared = 47138, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6157119 0.7124078

Amazon vs Pantanal
prop.test(c(3074476, 171808), c(4993368, 199688))
X-squared = 49048, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6157119 0.8603822

Amazon vs Pampa
prop.test(c(3074476, 132680), c(4993368, 235997))
X-squared = 2719.5, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6157119 0.5622105

Cerrado vs Caatinga
prop.test(c(1906416, 729425), c(2650259, 1049346))
X-squared = 2150.4, df = 1, p-value < 2.2e-16
sample estimates:
 prop 1   prop 2
0.7193320 0.6951234

Cerrado vs Atlantic forest
prop.test(c(1906416, 1081309), c(2650259, 1517823))
X-squared = 227.91, df = 1, p-value < 2.2e-16
sample estimates:
 prop 1   prop 2
0.7193320 0.7124078

Cerrado vs Pantanal
prop.test(c(1906416, 171808), c(2650259, 199688))
X-squared = 18709, df = 1, p-value < 2.2e-16
sample estimates:
 prop 1   prop 2
0.7193320 0.8603822

Cerrado vs Pampa
prop.test(c(1906416, 132680), c(2650259, 235997))
X-squared = 25798, df = 1, p-value < 2.2e-16
sample estimates:
 prop 1   prop 2
 0.7193320 0.5622105

Caatinga vs Atlantic forest
prop.test(c(729425, 1081309), c(1049346, 1517823))
X-squared = 891.74, df = 1, p-value < 2.2e-16
sample estimates:
 prop 1   prop 2
0.6951234 0.7124078

Caatinga vs Pantanal
prop.test(c(729425, 171808), c(1049346, 199688))
X-squared = 22803, df = 1, p-value < 2.2e-16
sample estimates:
  prop 1   prop 2
0.6951234 0.8603822

Caatinga vs Pampa
prop.test(c(729425, 132680), c(1049346, 235997))
X-squared = 15411, df = 1, p-value < 2.2e-16
sample estimates:
  prop 1   prop 2
0.6951234 0.5622105

Atlantic forest vs Pantanal
prop.test(c(1081309,171808), c(1517823,199688))
X-squared = 19586, df = 1, p-value < 2.2e-16
sample estimates:
  prop 1   prop 2
0.7124078 0.8603822

Atlantic forest vs Pampa
prop.test(c(1081309,132680), c(1517823,235997))
X-squared = 21625, df = 1, p-value < 2.2e-16
sample estimates:
  prop 1   prop 2
0.7124078 0.5622105

Pantanal vs Pampa
prop.test(c(171808,132680), c(199688, 235997))
X-squared = 45694, df = 1, p-value < 2.2e-16
sample estimates:
  prop 1   prop 2
0.8603822 0.5622105

Conclusion: Provision potential of ecosystem services related to nectarivory is differentially represented across Brazil.

CARNIVORY

Amazon vs Cerrado
prop.test(c(3331998, 1637283), c(4993375, 2650259))
X-squared = 18651, df = 1, p-value < 2.2e-16
 prop 1   prop 2

0.6672838 0.6177823

Amazon vs Caatinga
prop.test(c(3331998, 786580), c(4993375, 1049346))
X-squared = 27066, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6672838 0.7495907

Amazon vs Atlantic forest
prop.test(c(3331998, 1110186), c(4993375, 1517822))
X-squared = 22095, df = 1, p-value < 2.2e-16
 prop 1   prop 2
0.6672838 0.7314336

Amazon vs Pantanal
prop.test(c(3331998, 154217), c(4993375, 199687))
X-squared = 9595.3, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6672838 0.7722936

Amazon vs Pampa
prop.test(c(3331998, 192603), c(4993375, 236006))
X-squared = 22711, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6672838 0.8160937

Cerrado vs Caatinga
prop.test(c(1637283, 786580), c(2650259, 1049346))
X-squared = 57806, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6177823 0.7495907

Cerrado vs Atlantic forest
prop.test(c(1637283, 1110186), c(2650259, 1517822))
X-squared = 55486, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.6177823 0.7314336

Cerrado vs Pantanal
prop.test(c(1637283, 154217), c(2650259, 199687))
X-squared = 18989, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6177823 0.7722936

Cerrado vs Pampa
prop.test(c(1637283, 192603), c(2650259, 236006))
X-squared = 36727, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.6177823 0.8160937

Caatinga vs Atlantic forest
prop.test(c(786580, 1110186), c(1049346, 1517822))
X-squared = 1060, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.7495907 0.7314336

Caatinga vs Pantanal
prop.test(c(786580, 154217), c(1049346, 199687))
X-squared = 465.06, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7495907 0.7722936

Caatinga vs Pampa
prop.test(c(786580, 192603), c(1049346, 236006))
X-squared = 4695.6, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7495907 0.8160937

Atlantic forest vs Pantanal
prop.test(c(1110186, 154217), c(1517822, 199687))
X-squared = 1516.8, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7314336 0.7722936

Atlantic forest vs Pampa
prop.test(c(1110186, 192603), c(1517822, 236006))
X-squared = 7662.6, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7314336 0.8160937

Pantanal vs Pampa
prop.test(c(154217, 192603), c(199687, 236006))
X-squared = 1277.7, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7722936 0.8160937

Conclusion: Provision potential of ecosystem services related to carnivory is differentially represented across Brazil.

ALL BATS

Amazon vs Cerrado
prop.test(c(4145303, 2147622), c(4993365, 2650258))
 X-squared = 4673.7, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8301622 0.8103445

Amazon vs Caatinga
prop.test(c(4145303, 765871), c(4993365, 1049347))
X-squared = 57326, df = 1, p-value < 2.2e-16

prop 1   prop 2
0.8301622 0.7298549

Amazon vs Atlantic forest
prop.test(c(4145303, 1092403), c(4993365, 1517821))
X-squared = 90245, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8301622 0.7197179

Amazon vs Pantanal
prop.test(c(4145303, 154939), c(4993365, 199688))
X-squared = 3969.9, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8301622 0.7759054

Amazon vs Pampa
prop.test(c(4145303, 180700), c(4993365, 235988))
X-squared = 6548.5, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8301622 0.7657169

Cerrado vs Caatinga
prop.test(c(2147622, 765871), c(2650258, 1049347))
X-squared = 29103, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8103445 0.7298549

Cerrado vs Atlantic forest
prop.test(c(2147622, 1092403), c(2650258, 1517821))
X-squared = 45796, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.8103445 0.7197179

Cerrado vs Pantanal
prop.test(c(2147622, 154939), c(2650258, 199688))
X-squared = 1419.1, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8103445 0.7759054

Cerrado vs Pampa
prop.test(c(2147622, 180700), c(2650258, 235988))
X-squared = 2767.3, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.8103445 0.7657169

Caatinga vs Atlantic forest
prop.test(c(765871, 1092403), c(1049347, 1517821))
X-squared = 318.89, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7298549 0.7197179

Caatinga vs Pantanal
prop.test(c(765871, 154939), c(1049347, 199688))
X-squared = 1836.2, df = 1, p-value < 2.2e-16
 prop 1   prop 2
 0.7298549 0.7759054

Caatinga vs Pampa
prop.test(c(765871, 180700), c(1049347, 235988))
X-squared = 1276.4, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7298549 0.7657169

Atlantic forest vs Pantanal
prop.test(c(1092403, 154939), c(1517821, 199688))
X-squared = 2802, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7197179 0.7759054

Atlantic forest vs Pampa
prop.test(c(1092403, 180700), c(1517821, 235988))
X-squared = 2171.7, df = 1, p-value < 2.2e-16
prop 1   prop 2
0.7197179 0.7657169

Pantanal vs Pampa
prop.test(c(154939, 180700), c(199688, 235988))
X-squared = 63.416, df = 1, p-value = 1.673e-15
prop 1   prop 2
0.7759054 0.7657169

Conclusion: Provision potential of ecosystem services related to all bats is differentially represented across Brazil.

Table S6. Proportional losses associated to bats of different size classes

	Carnivory		Nectarivory			Frugivory		
	M	**G**	**S**	**M**	**G**	**S**	**M**	**G**
Amazon	0.141	0.141	0.161	0.271	0.197	0.12	0.177	0.17
Cerrado	0.619	0.619	0.581	0.45	0.611	0.531	0.608	0.594
Caatinga	0.443	0.443	0.386	0.335	0.423	0.4	0.414	0.404
Atlantic forest	0.717	0.717	0.72	0.749	0.686	0.738	0.719	0.717
Pantanal	0.17	0.17	0.232	0.225	0.228	0.243	0.211	0.197
Pampa	0.444	0.445	0.435	0.377	0.421	0.446	0.446	0.462
Brazil	0.474	0.474	0.336	0.42	0.495	0.316	0.387	0.422

Cont.

	Insectivory			All bats		
	S	**M**	**G**	**S**	**M**	**G**
Amazon	0.174	0.179	0.158	0.152	0.194	0.17
Cerrado	0.553	0.6	0.594	0.559	0.606	0.57
Caatinga	0.394	0.407	0.388	0.418	0.41	0.401
Atlantic forest	0.715	0.701	0.731	0.721	0.713	0.71
Pantanal	0.182	0.187	0.163	0.216	0.191	0.193
Pampa	0.478	0.441	0.509	0.454	0.449	0.45
Brazil	0.375	0.473	0.43	0.33	0.412	0.421

S = Small
M = Medium
L = Large