Mammal diversity, threats and knowledge across spatial scales

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ABSTRACT

Spatial scale is a fundamental consideration in planning for biodiversity conservation. Limited resources means that decision and policy makers often take a triage approach to biodiversity conservation, addressing the most pressing issues first and then proceeding as resources allow. At the global scale, where international treaties and multinational planning are necessary – it is important to have access to the best data available and to unbiased and comprehensive analysis. However few conservation actions can be performed at the global scale, and it becomes increasingly important to be able to "zoom in" to prioroty countries or regions to implement policy or other decisions. At regional scales, regulations can be put into place, protected areas can be designated and other broad reaching actions – but still finer scales are necessary to implement effective management of areas or species. From the regional scale we can prioritize sites for specific treatments or actions, and thus scale down even further to be able to manage populations, parks, watersheds or species. Herein we provide a global dataset and analysis framework to address declines in mammal populations and ultimately extinction risk. By making this data freely and publically available we hope that it can bring the best science to bear on decision making globally and nationally. Protected areas are among the most powerful tools available to protect species and populations within and between countries – thus at the regional scale we examine the effectiveness of land stewardship on mammal populations. Because protected areas alone are seldom large enough to retain large mammal populations, we then evaluated the utility of a biological corridor, at the landscape scale, in providing linkage between protected areas. Finally we examine this same landscape in terms of the need to broaden our ecological decision making parameters to include terrestrial, freshwater and marine components – and explore means by which ecological services transcend these biomes and why decision making need take all into consideration. We conclude that spatial scale is a fundamental issue that is often neglected in decision making and that in many cases conservation planning recommendations are either too broad or too specific in the context of the policy tools available.

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DISSERTATION INTRODUCTION

Spatial scale is a fundamental consideration in planning for biodiversity conservation. Ecologically, systems are structured at hierarchical scales and linked through various processes. Intact ecological processes can provide services to humans as well as to biodiversity, and understanding the flows between systems and across scales is important for the conservation of all life on Earth. Biodiversity conservation is scale dependent, as interactions within and among biomes, ecosystems and species can be global (climate change) or site specific (pollution). When species are the target of conservation, knowing their global status and distribution can be critical in determining regional and site priorities. Social systems are also organized at hierarchical scales, such that policy can be international, national or regional. Herein we explore three spatial scales in mammal conservation, and at each scale discuss the ecological and planning framework needed to target resources, policies and actions. We also explore thematic scales, and how to move beyond the entrenched disciplinary concepts of terrestrial, freshwater and marine to a more comprehensive and unified approach.

Chapter 1 addresses mammal diversity, threats and the state of knowledge at the global scale. In this chapter we assess all terrestrial and marine mammals for their global IUCN Red List threat status, and thereby establish the context for regional and site conservation efforts. With information on the global status of each species and their distributions, we can ask the question: “where should we be focusing conservation resources to prevent mammal extinctions?” We have provided several analyses which will help practitioners begin to curb future mammal extinctions and identify priority actions to reduce threats. For each of the 5,487 mammalian species we provide detailed information on the habitats and ecology, distribution, threats, conservation measures and extinction risk. We then summarize the data to evaluate global trends in species richness, phylogenetic diversity, restricted range species and median range size of species. Finally we provide an analysis of the global patterns of threat, including habitat loss, harvesting, accidental mortality (by catch) and pollution. The importance of establishing the global context for mammal conservation is that in order to prevent species extinctions we need to know which species are most threatened, where they occur and what threats are driving species declines. With this information we can make more precise decisions about where to focus scarce resources.

In Chapter 2 we scale down from the global to regional scale, focusing on the Talamanca Mountains in Central America. The Talamancas are a region of high phylogenetic diversity, containing a high number of restricted range species, and species threatened by habitat loss, according to the global analysis. Regionally we focused our efforts on larger mammals, which are more sensitive to large scale habitat loss and harvesting than smaller mammals, and on Costa Rica. We use camera traps to collect data on species richness, diversity and relative abundance among protected and non-protected sites in lowland and montane tropical forests in Talamanca, Costa Rica. We use these data to evaluate the effectiveness of various stewardship types on the conservation of medium and large mammals in tropical forests. Our data suggests that forests that occur in protected areas are not more effective than private forests at retaining diverse and abundant mammal assemblages. We also demonstrate that private properties that enforce existing hunting laws retain more diverse and abundant mammal communities than protected areas generally. At the regional scale we can much more easily translate science to policy, and in this case we chose Costa Rica both for logistical reasons and so that we can provide feedback on existing management and conservation policy in the Talamanca Mountains. Today the Talamancas are a habitat island, and the surrounding lowlands have been cleared, confining species to the mountains. The majority of the remaining habitat lies within protected areas and Indigenous Territories, but illegal hunting is occurring everywhere due to lack of enforcement. Currently national policies concerning hunting need revision, and the protected areas of the Talamancas need sufficient resources to enforce current policy.

On the Caribbean slopes of the Talamanca Mountains are a mosaic of protected areas, Indigenous Territories and private lands which stretch from the La Amistad National Park to the sea. This transect spans the human dominated landscapes surrounding the core of the Talamanca Mountains, contains the most important remnants of lowland forest remaining in the region and is the site of the Talamanca-Caribbean Biological Corridor. In Chapter 3 we used data collected over 14 months of camera-trapping and local interviews to ask four overarching questions: 1) Are protected areas enough to conserve mammals in the corridor? 2) Is there a relationship between hunting and wildlife abundance and diversity? 3) What impact does wildlife conflict have on mammal populations? and 4) What impact does hunting have on mammal populations? Our results indicate that protected areas alone are not enough to conserve mammals, especially in a human-dominated landscape, and that the majority of mammal communities are highly modified due to hunting pressure. In these fragmented remnants of lowland rainforests, the majority of large mammals have been extirpated due to habitat loss and fragmentation, hunting, and human infrastructure (roads and houses). At this scale, there are numerous options for curbing the current trends which are simplifying mammal communities, and there is an organization in place which works across the public and private sectors. Therefore we are able to make broad policy recommendations (to control hunting and deforestation) but also more targeted recommendations about which communities to focus on for education, which areas most need restoration, and which species to target for conservation. For example, whereas the Jaguar is a clear conservation target at the regional scale, the possibility of its persistence in a human dominated landscape is very low – as efforts to conserve large carnivores in this landscape will create more conflict and ultimately result in less community level cooperation. Where humans are dominant, landscape scale conservation is community driven and conservation efforts must be considered at this scale.

Many rural communities within the Caribbean lowlands of the Talamancas require ecosystem services for health and well being. Ecosystem services necessitate intact ecosystems, and ecosystems span the terrestrial, freshwater and marine realms. In Chapter 4 we examine linkages between these realms and discuss how systematic conservation planning can begin to address ecological processes, many of which lead to improved ecosystem services. Although the chapter focuses on the broad concepts and challenges of strategic planning between terrestrial and aquatic systems, we ultimately focus a case study on the Sixaola River Basin, within the TalamancaCaribe region and suggest means to integrate resource conservation with economic benefit to local communities and individual families. Finally we discuss the current suite of available methods for integrating conservation planning across terrestrial and aquatic realms and discuss how this could be applied to a landscape such as the Talamanca-Caribe. We conclude that although the majority of the Sixaola River basin is protected, the unprotected lowland areas are those that support the greatest biodiversity. Extensive banana plantations, for example, have removed (illegally) the riparian forests and thus discharge sediments and pollutants (pesticides) directly into the most productive portion of the river basin, which then moves these contaminants to the ocean and deposits them on the most productive region of the coastline – the coral reefs. Even though the majority of the region (spatially) is protected, the ecological processes which sustain it are not. In this case the biodiversity of an entire watershed, including the nearshore marine systems, can be severely impacted by a single persistent threat – banana plantations on the floodplains. However the consequences of this threat go beyond biodiversity to impacting human health and both ecosystem processes and services.

In these four chapters we explore issues of spatial scale in conservation planning. Although our research focuses on mammals, these issues of scale are important considerations across ecological, political and social systems. When designing conservation projects it is very important to ensure that the scale of the project is appropriate for the species being targeted and the resources available. In addition, when targeting resources for human development projects it is equally important to understand the scales of ecological processes which will impact ecosystem services.

Chapter One

The status of the world's land and marine mammals: diversity, threat, and knowledge **

Abstract:

Knowledge of mammalian diversity is still surprisingly disparate, regionally and taxonomically. Here, we present the results of the most comprehensive assessment to date of the conservation status and distribution of the world's mammals. Data, compiled by 1,700+ experts, cover all 5,487 species, including for the first time marine mammals. Global macroecological patterns are very different for land and marine species, but suggest common mechanisms driving diversity and endemism across systems. Compared to land species, threat levels are higher among marine mammals, driven by different processes (accidental mortality and pollution, rather than habitat loss), and spatially distinct (peaking in northern oceans, rather than in Southeast Asia). Marine mammals are also disproportionately poorly known. These data are made freely available to support further scientific developments and conservation action.

Introduction

Mammals play key roles throughout many of the world's ecosystems, including grazing, predation, and seed dispersal. They also provide important human benefits such as food, recreation, and income. Nonetheless, our understanding of mammals is surprisingly patchy, particularly for the smaller and more inconspicuous species, and in the least-studied (often species-rich) parts of the world. Indeed, the rate of species discovery among mammals is still high, and most of the recently described species occur in regions of high levels of endemism and threat (Reeder et al. 2007). It is therefore possible that mammal species are being lost even before their existence has been documented.

An assessment of the conservation status of all known mammals was last undertaken by the International Union for Conservation of Nature (IUCN) in 1996 (IUCN 1996). These

IUCN Red List classifications of extinction risk have been used in numerous studies, including the identification of traits associated with high extinction risk (Purvis et al. 2000, Cardillo et al. 2005), prediction of future species' losses (Cardillo et al. 2006), and prioritization of species for conservation action (Isaac et al. 2007). Although the 1996 assessment was a remarkable feat at the time, it provided very little supporting data to justify the status attributed to each species, and was based on categories and criteria that have now been superseded. Furthermore, IUCN Red List assessments are officially outdated after 10 years, and about 3,300 mammals assessed in 1996 had fallen into this category by 2006.

Global distribution maps for all terrestrial mammals have been compiled by Sechrest (2003) (4,735 species) and Ceballos and colleagues (2005) (4,818 species). Their data have been used in a variety of analyses, including recommending global conservation priorities (Ceballos et al. 2005, Ricketts et al. 2005, Ceballos and Ehrlich 2006, Carwardine et al. 2008, Davies et al. 2008), analyzing the coverage of protected areas (Rodrigues et al. 2004), assessing cross-taxon surrogacy (Grenyer et al. 2006), and investigating spatial patterns of mammalian evolution (Davies et al. 2008). Many of these maps were, however, compiled from very coarse data on species' distributions, and were not consistently subjected to expert review. Nearly 700 currently recognized species, including marine mammals, were not covered in any previously published analyses. Furthermore, these datasets were not made publicly available to the scientific and the conservation communities.

Here, we present the results of the most comprehensive assessment to date of the conservation status and distribution of the world's mammals. These data cover a total of 5,487 wild species recognized as extant since 1500, including, for the first time, all marine mammals. Compiled over five years, these assessments are the culmination of an IUCN-led collaborative effort of over 1,700 experts from more than 130 countries. For each species detailed information is provided on taxonomy, distribution, habitats and ecology, threats, human use, population trends, and conservation measures. All data are freely available for consultation and downloading at a dedicated internet portal (IUCN

2009). Here, we build on these data to investigate global patterns of diversity, threat and knowledge for mammals across the world's land and seas.

Diversity

Mammals are a highly versatile group that includes some of world's fastest runners, deepest divers, and most agile fliers, having colonized most of the Earth's habitats. Land species (i.e., terrestrial, including volant, and freshwater) are concentrated in the tropical and subtropical moist broadleaf forests of Central and South America (25% of the species), of South and Southeast Asia (21%) and of sub-Saharan Africa (19%). As in previous studies (Ceballos et al. 2006, Grenyer et al. 2006), we found particularly high levels of species richness in the Amazonian slopes of the Andes and in several Afromontane regions in Africa, such as the Albertine Rift, but we also report extremely high levels of diversity in Asia, most noticeably the Hengduan Shan mountains of southwestern China, Peninsular Malaysia, and Borneo (Fig. 1A). This Asian 'peak,' validated by data collected through several expert workshops in the region, reflects a real improvement in data quality and quantity relative to previous studies (Sechrest 2003, Ceballos et al. 2006). Because the distribution of many large mammal species has recently contracted substantially in tropical Asia, much more so than in either Africa or South America (Morrison et al. 2007), local diversity was once undoubtedly even higher in Asia. Overall, the species richness pattern for land mammalian species is similar to that found for birds and amphibians (Grenyer et al. 2006), suggesting that mammal species diversity is similarly driven by energy availability and topographic complexity (Hawkins and Diniz-Filho 2006, Davies et al. 2007).

Marine mammals occupy open waters in all oceans and seas, with high species richness in tropical and temperate coastal platforms adjacent to all continents, as well as in offshore areas in the Tasman and Caribbean seas, east of Japan and New Zealand, west of Central America, and in the southern Indian Ocean. While richness of land species generally peaks towards the equator, marine diversity peaks at around 40° N and S, corresponding to belts of high oceanic productivity (Field et al. 1998). For both land and marine species, therefore, richness seems to be associated with primary productivity. An interesting exception is the low species richness in the North Atlantic Ocean in relation to its high productivity (Field et al. 1998). Only two species extinctions are recorded from this region – Sea Mink (*Neovison macrodon*; Campbell 1988) and Gray Whale (*Eschrichtius robustus*; Bryant 1995) – but historical records of species exploitation in places where they no longer occur provide evidence for many local extinctions, for example of Harp Seal in the Baltic Sea (*Phoca groenlandica*; Stora and Ericson 2004), of Bowhead Whales off Labrador (*Balaena mysticetus*; McLeod et al. 2008), and of Walrus in Nova Scotia (*Odobenus rosmarus*; Reeves 1978). Environmental changes may have played a role in these and other extinctions, but this raises the hypothesis that past human exploitation of marine mammals may have left a mark on current patterns of species richness – also likely to be the case with land mammal diversity in regions such as Australia (Turney et al 2008) and the Caribbean (Turvey et al. 2007a).

Phylogenetic diversity is a measure that takes account of phylogenetic relationships (and hence evolutionary history) between taxa (Faith 1992). It generally increases with local species richness, but for the same number of species it is higher if species are less related to each other. It is therefore less affected by variations in the taxonomic classification than species richness, and is arguably a more relevant currency of diversity, because it measures the raw material on which future evolutionary processes will operate. We found that local species richness (Fig. 1A) and phylogenetic diversity (Fig. 1B) are very closely related for land species (r^2=0.98). The relationship is not as close in the marine environment (r^2=0.73), with disproportionately high phylogenetic diversity in the southern oceans. This pattern suggests that either southern marine species tend to be less related than elsewhere, or that current species may in fact be poorly known complexes of multiple species, with new species awaiting discovery. The latter contention is consistent with the fact that two-thirds of marine species that are classified as Data Deficient (with insufficient information to assess threat status) occur in this area.

Among land mammals the size of species' ranges varies from a few hundred square meters for the Bramble Cay Melomys (*Melomys rubicola*) in Australia, to 64.7 million km^2 across Eurasia and North America for the Red Fox (*Vulpes vulpes*). Within marine species, the smallest range (16,500 km^2) is that of the Vaquita (*Phocoena sinus*), endemic to the northern Gulf of California, while the pan-oceanic Killer Whale (*Orcinus orca*) is the most widespread mammal with a 350-million-km^2 range. Despite these extremes, most species have small ranges: the majority of land taxa occupy an area smaller than the United Kingdom (median range size: 193,600 km^2) and the range size of most marine mammals is less than one-fifth the area of the Indian Ocean (median range size: 14.5 million km^2).

Among land mammals restricted-range species (those 25% of species with the smallest ranges; first quartile: 17,700 km^2) are concentrated on high diversity islands (such as Madagascar, Sri Lanka, New Guinea, Japan, Sulawesi and the Philippines), as well as in tropical mountain systems (such as the New Guinea Highlands, Himalayas, Western Ghats of India, Eastern Arc Mountains, Ethiopian Highlands, Andes, and Sierra Madres in Mexico) (Fig. 1C). Marine restricted-range species (first quartile: 3.8 million km^2) are almost entirely found around continental platforms, particularly in highly productive areas, with the main peak off the Southern Cone of South America (Fig. 1C). Both land and marine patterns of endemism are thus apparently associated with highly productive areas subject to strong environmental gradients (altitudinal in land; depth in marine).

A different perspective on patterns of species' endemism is obtained by mapping global variation in the median range size of all species that occur at a given location (Fig. 1D). Here the results are not dominated by a few rare species (as in Fig. 1C) but are representative of the overall local mammalian communities. For land species there is a strong association between the longitudinal width of landmasses and the median range size of species: the largest ranges tend to be found across the widest part of each continent, particularly in northern Eurasia, while islands (e.g., Madagascar, and those in Southeast Asia and the Caribbean) and narrow continental areas (e.g., southern North and South America, southern Africa) tend to have species with smaller ranges. Superimposed on this general pattern, species ranges also tend to be restricted in areas of high topographic complexity (e.g., the Rockies, Andes, and the Himalayas). These results agree with those found for birds, suggesting that range areas are constrained by the availability of land area within the climatic zones to which species are adapted (Hawkins and Diniz-Filho 2006, Orme et al. 2006). Among marine species, small median range sizes are found around the continental platforms, suggesting that (as with land species) steep environmental gradients (here, associated with depth) determine species distributions. However, the global marine pattern is dominated by a latitudinal effect, with median species ranges generally declining towards both poles, perhaps reflecting the latitudinal gradient in the overall ocean area. As with previous studies (Hawkins and Diniz-Filho 2006, Orme et al. 2006), we found no support for the so-called Rapoport rule (Stevens 1989) that species' range sizes decline with latitude.

Threat

Twenty-five percent (*n*=1139) of all mammals for which the conservation status is known are threatened with extinction (i.e., Vulnerable, Endangered or Critically Endangered; Table 1). The exact percentage of threat is not known because the status of 836 Data Deficient species could not be determined, but it is somewhere between 21% (assuming no Data Deficient species are threatened) and 36% (assuming all Data Deficient species are threatened). The conservation status of marine species is of particular concern, with an estimated 36% (minimum 23%, maximum 61%) of species threatened. This analysis supports concerns that marine systems are even more threatened than those in terrestrial habitats (Carpenter et al. 2008).

In all, 188 mammal species were classified as Critically Endangered: they face a very high probability of extinction within the next few years. For 29 of these species, it may already be too late: species like the Baiji or Yangtze River Dolphin (*Lipotes vexillifer*) are flagged as 'Possibly Extinct' because there is only a very small chance that any still remain (Turvey et al. 2007b). For the 76 species classified as Extinct (since 1500), there is no reasonable evidence to suggest that they still exist. Two other species, Scimitar-horned Oryx (*Oryx dammah*) and Père David's Deer (*Elaphurus davidianus*), persist only in captivity (Extinct in the Wild; Table 1).

Species not classified as threatened are not necessarily safe. Many have experienced large range and population declines in the past (e.g. Gray Wolf *Canis lupus*, Brown Bear *Ursus arctos*), which are not accounted for in their current Red List status (Morrison et al. 2007). About 6% of the mammals are classified as Near Threatened – close to qualifying for, or likely to qualify for, a threatened category in the near future (Table 1). Moreover, 52% of all species for which population trends are known are declining, including 22% of those classified as Least Concern. These trends indicate that the overall conservation status of mammals will likely deteriorate further in the near future, unless appropriate conservation actions are put in place. On a positive note, 5% of currently threatened species are known to have stable or increasing populations, indicating that they are recovering from past threats (e.g., European Bison *Bison bonasus* and Black-footed Ferret *Mustela nigripes*).

Among land mammals, the pattern of distribution of threatened species is dominated by the extraordinary concentration in South and Southeast Asia (Fig. 2A). Among primates, for example, a staggering 79% (minimum 76%, maximum 80%) of all species in this region are threatened with extinction. Other peaks of threat are found in the tropical Andes, southern Mexico, the Upper Guinea region in West Africa, the Cameroonian Highlands, the Albertine Rift, Madagascar, and the Western Ghats in India. All of these regions correspond to areas of high species richness (Fig. 1A) and endemism (Figs. 1B,C) that are subject to high human pressure (Sanderson et al. 2002). Among marine species, peaks of threat are found in the North Atlantic and the North Pacific, as well as in insular Southeast Asia, all of which are areas of high endemism (Fig. 1C) and of high human impact (Halpern et al. 2008). Low threat levels in the southern hemisphere may reflect a historical pattern (given that these oceans became heavily exploited much more recently), but they may also reflect a lack of knowledge (as 46% of the species in this region are Data Deficient).

Worldwide, mammalian species face numerous threats (Reynolds et al. 2005). Habitat loss and degradation (affecting 40% of all species assessed) and harvesting (hunting/gathering for food, medicine, fuel and materials; affecting 17%) are by far the main threats to mammals, but their relative importance varies across regions and across taxa (Figs. 2B,C). Among land species, habitat loss is prevalent across the tropics, driven particularly by deforestation in Central and South America, West, East and Central Africa, Madagascar, and in South and Southeast Asia (Fig. 2B) (Achard et al. 2002). Harvesting is having particularly devastating effects on mammal populations in Asia, but as evidenced by the global bushmeat crisis (Robinson and Bennett 2004), African and South American species are also affected (Fig. 2C). Large mammals (orders Cetartiodactyla, Primates, Perissodactyla, Proboscidea and Carnivora) are disproportionately threatened by harvesting, which affects 90% of all large mammals in Asia, 80% in Africa and 64% in the Neotropics (compared to 28%, 15% and 11% of small mammals, respectively).

Among marine mammals, the dominant threat is accidental mortality (78% of all species), particularly through fisheries by-catch and vessel strike. While coastal areas are the most affected (Fig. 2D), accidental mortality also threatens species in off-shore waters where particular types of gear are operated (e.g., purse seines in the eastern tropical Pacific). Pollution (60% of all species), is the second most prevalent threat (Fig. 2E), but this designation includes a diversity of mechanisms, such as chemical contaminants, marine debris, noise, and climate change. Sound pollution, particularly by military sonar use, has been implicated in mass strandings of cetaceans (Reynolds et al. 2005), and climate change is already having an impact on sea ice dependent species (e.g. Polar Bear *Ursus maritimus* and Harp Seal *Pagophilus groenlandicus*). Despite progress through international agreements, harvesting remains a major threat for marine mammals, affecting more than 50% of species, particularly in coastal areas (Fig. 2C). Among all mammals, disease affects relatively few species (2%), but it has led to catastrophic declines in some, most dramatically the Tasmanian Devil (*Sarcophilus harrisii*), threatened by facial tumor disease (McCallum 2008).

Threat levels are not uniform across mammalian groups (Fig. 3). Those with significantly ($p<0.01$) higher than expected incidence of threatened or extinct species include several primate families (Primates), two deer families (Moschidae, Cervidae), bovids (Bovidae), tapirs (Tapiridae), bears (Ursidae), pigs (Suidae), hippos (Hippopotamidae), hutias (Capromyidae), potoroids (Potoroidae), golden moles (Chrysochloridae), Old World fruit bats (Pteropodidae) and the West Indian shrews (Nesophontidae, all extinct). Families less threatened than expected include some of small bats (Chiroptera) and rodents (Rodentia), moles (Talpidae), and opossums (Didelphidae).

A positive relationship has been reported between body size and threat among mammals (Purvis et al. 2000, Cardillo et al. 2005), and indeed we found that the most threatened mammalian groups are dominated by large species, such as primates and ungulates, while the least threatened include small mammals such as rodents and bats. Larger species tend to have lower population densities, slower life histories, larger home ranges, and are more likely to be exploited by humans – factors which puts them at greater risk (Cardillo et al. 2005). Among smaller species, habitat loss is the dominant threat (Entwistle and Dunstone 2000), and their conservation status tends to be determined mainly by the size and location of their range (Cardillo et al. 2005). However, the relationship between body size and extinction risk is not straightforward, and some families of small mammals (e.g., golden moles, West Indian shrews) are also highly threatened. As with a previous study (Entwistle and Dunstone 2000), we found that while large mammals have a significantly higher fraction of their species that are either threatened or extinct (χ^2~0; p<0.0001), they have suffered similar levels of extinction to small mammals (χ^2=0.74; n.s.).

Knowledge

Although mammals are among the best known organisms, they are still being discovered at surprisingly high rates, some estimating that an additional 2,000 species have yet to be discovered (Reeder et al. 2007). The number of recognized species has increased by 19% since 1992, including 349 newly described species, along with taxonomic revisions resulting in 512 taxa being elevated to, or revalidated as, species. The spatial pattern of new species description (Fig. 4A) reflects the interaction between the local state of knowledge and taxonomic effort. Peaks in Madagascar and the Amazon can be explained by relatively high, recent taxonomic activity in these poorly-known areas, while the lack of new species in Africa (and particularly in the poorly surveyed Congo Basin) may reflect more limited efforts there.

Newly described species are more poorly-known (44% are Data Deficient, compared to 13% in species described pre-1992) and also disproportionately threatened (51% of non-Data Deficient species are threatened, compared to 25% for other species). This reinforces the concern that mammalian species may be vanishing even before they are known to science. Newly described species provide an indication of areas where knowledge has increased in the recent past (Fig. 4A), whereas Data Deficient species highlight regions known to be in need of future research (Fig. 4B). Most land species are concentrated in tropical forests (Fig. 4B), reflecting species richness patterns (Fig. 1A). In the Amazon and Congo basins, which are still relatively unaffected by human activity, Data Deficient species are less likely to be threatened, but in the Atlantic Forest, West Africa and Borneo, where natural habitats are vanishing very rapidly (Achard et al. 2002), many Data Deficient species may be dangerously close to extinction.

Marine species are less well-known than land mammals – 38% are listed as Data Deficient (Table 1). Some species of pinnipeds that breed on land are better studied, because as long as their breeding locations are known their populations can be monitored directly. By comparison, populations of whales, dolphins, porpoises and sirenians are so difficult to survey that declines that should result in a Vulnerable listing would go undetected at least 70% of the time (Taylor et al. 2007). The diversity of marine Data Deficient species is particularly high along the Antarctic Convergence (Fig. 4B), largely driven by the beaked whales, 19 of which are listed as Data Deficient. A relative absence of Data Deficient species in the northern Atlantic and Pacific Oceans reflects the higher research effort and expertise applied to these areas, as well as a longer history of human exploitation.

Discussion

This is the first comprehensive assessment of every species in an entire Class (Mammalia) across land and marine systems. An unprecedented amount of standardized data has been compiled on the geography, ecology and population status of all mammalian species, through the collective knowledge of more than 1,700 experts. For many species these Red List data are now the best centralized source of information, and likely to become a first port of call for many researchers.

Our results paint a bleak picture of the global status of mammals worldwide. We estimate that one in four species is threatened with extinction, and that the population of one in two is declining. The situation is particularly serious for land mammals in Asia, through the combined effects of over-harvesting and habitat loss, and for marine species, victims of our increasingly intensive use of the oceans. Yet, more than simply reporting on the depressing status of the world's mammals, these Red List data can and should be used to inform strategies for addressing this crisis (Rodrigues et al. 2006), for example to identify priority species (Isaac et al. 2007) and areas (Cardillo et al. 2006, Ceballos and Ehrlich 2006, Rodrigues et al. 2004) for conservation. Further, these data can be used to indicate trends in the conservation status over time (Butchart et al. 2007). Despite a general deterioration in the status of mammals, our data also show that species recoveries are possibly through targeted conservation efforts. Appropriate knowledge is a key ingredient of conservation success, and we believe that by making these data freely and publicly available we are contributing to create the conditions for improving the conservation status of the world's mammals.

We also predict that these data will contribute to furthering understanding of mammalian biogeography, ecology, and evolution. As one of the first studies of global marine biodiversity patterns (Carpenter et al. 2008, Fuhrman et al. 2008), this assessment is a particularly valuable contribution to the young field of marine macroecology, The possibility to compare between marine and land patterns is particularly exciting, with similarities and differences shedding light on the ecological mechanisms behind observed patterns. We found that while the diversity of both land and marine mammals generally increases toward lower latitudes, it peaks at the equator for land species and around 40° N/S for marine species (Fig. 1A). Endemism, on the other hand, follows quite distinct patterns over land and the sea (Figs. 1C,D). And yet, for both groups the results preliminarily suggest that primary productivity drives patterns of species richness, while endemism seems to be associated with environmental gradients. Each of these patterns should be probed in greater depth in future research.

We trust that this paper serves as an incentive for increased use of these and other IUCN Red List data to expand ecological knowledge, and for guiding priorities and strategies for conserving the world's mammals. What prospect for humanity if we cannot avert the threat of irreplaceable loss of our closest relatives?

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Tables and Figures

Table 1: Number of species in each IUCN Red List Category and threat level for all mammals, and for land and marine species. Categories: EX – Extinct; EW – Extinct in the Wild; CR – Critically Endangered; VU – Vulnerable; EN – Endangered; LC – Least Concern; DD – Data Deficient. The threat level is calculated as (VU+EN+CR)/(Total – DD), with a range between (VU+EN+CR)/Total and (VU+EN+CR+DD)/Total.

	Total	**EX (%)**	**EW (%)**	**CR (%)**	**EN (%)**	**VU (%)**	**NT (%)**	**LC (%)**	**DD (%)**	**Threat level**
All mammals	**5487**	76	2	188	448	505	323	3109	836	25%
		(1.4)	(0.04)	(3.4)	(8.2)	(9.2)	(5.9)	(56.7)	(15.2)	(21 – 36%)
Land mammals	**5282**	not mapped		185	436	497	316	3071	777	25%
				(3.5)	(8.3)	(9.4)	(6.0)	(58.1)	(14.7)	(21 – 36%)
Marine mammals	**120**	not mapped		3	12	12	7	40	46	36%
				(2.5)	(10.0)	(10.0)	(5.8)	(33.3)	(38.3)	(23 – 61%)

Figure 1. Global patterns of mammalian diversity, for land (terrestrial and freshwater, *n*=5282; in brown) and marine (*n*=120; in blue) living species, on a hexagonal grid (each cell ~22,300 km^2). Seven species are mapped as both land and marine; 78 extinct and 14 Data Deficient species are not mapped. A) Species richness (number of species). B) Phylogenetic diversity (in millions of years). C) Number of restricted-range species (those 25% species with the smallest ranges land; land *n*=1321; marine *n*=20). D) Median range size of species in each cell (in million km^2).

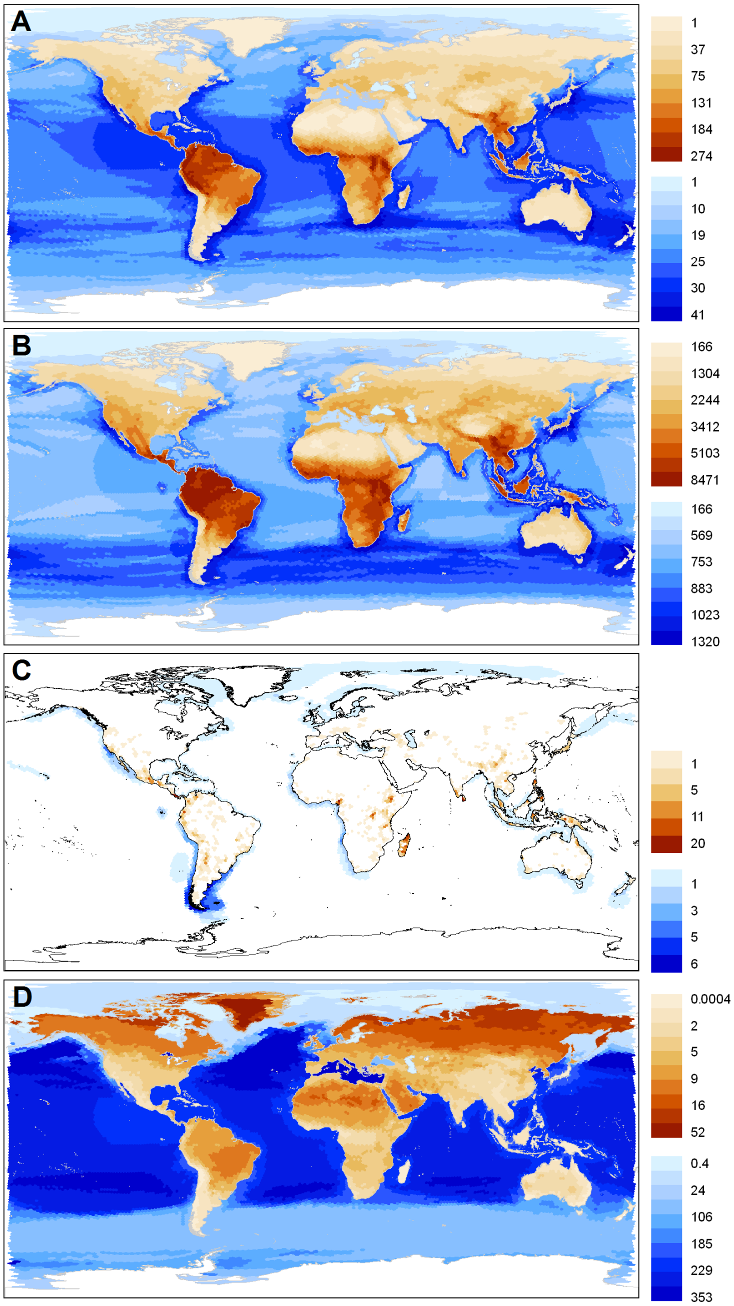


Figure 2. Global patterns of threat, for land (terrestrial and freshwater; brown) and marine (blue) mammals. A) Number of globally threatened species (Vulnerable, Endangered or Critically Endangered; land *n*=1118; marine *n*=27). Number of species affected by: B) habitat loss (land *n*=2016; marine *n*=20); C) harvesting (land *n*=872; marine *n*=61); D) accidental mortality (land *n*=193; marine *n*=98); E) pollution (land *n*=151; marine *n*=75). The color scale is the same for B, C, D and E so these maps are directly comparable.

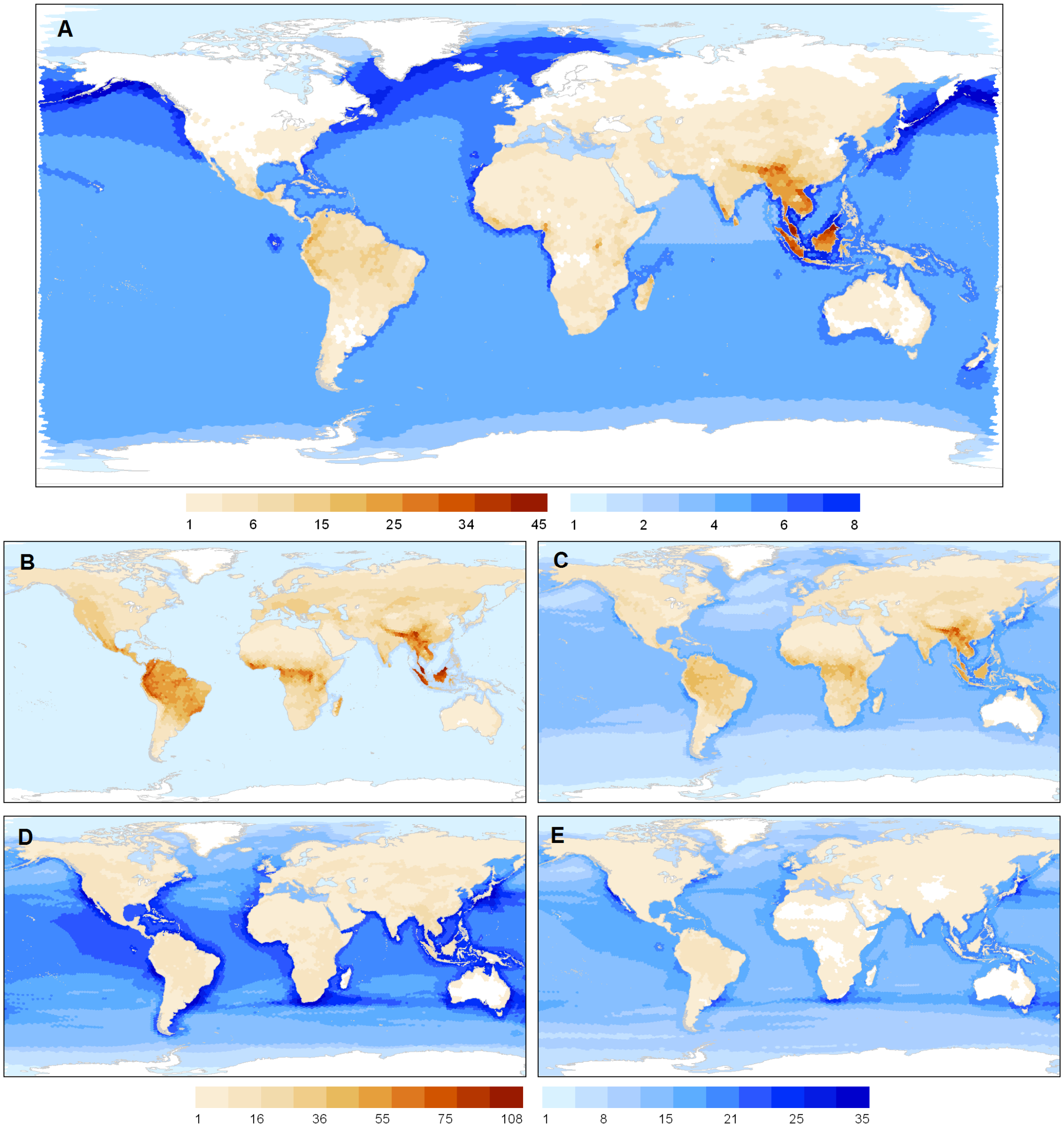
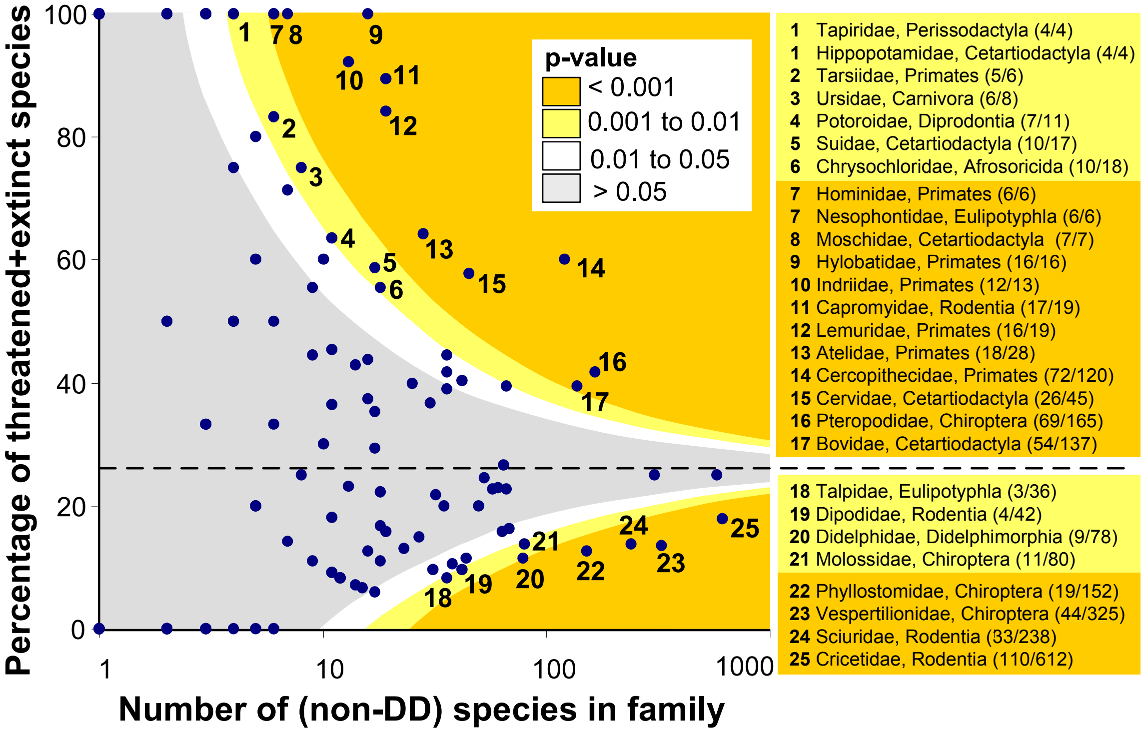
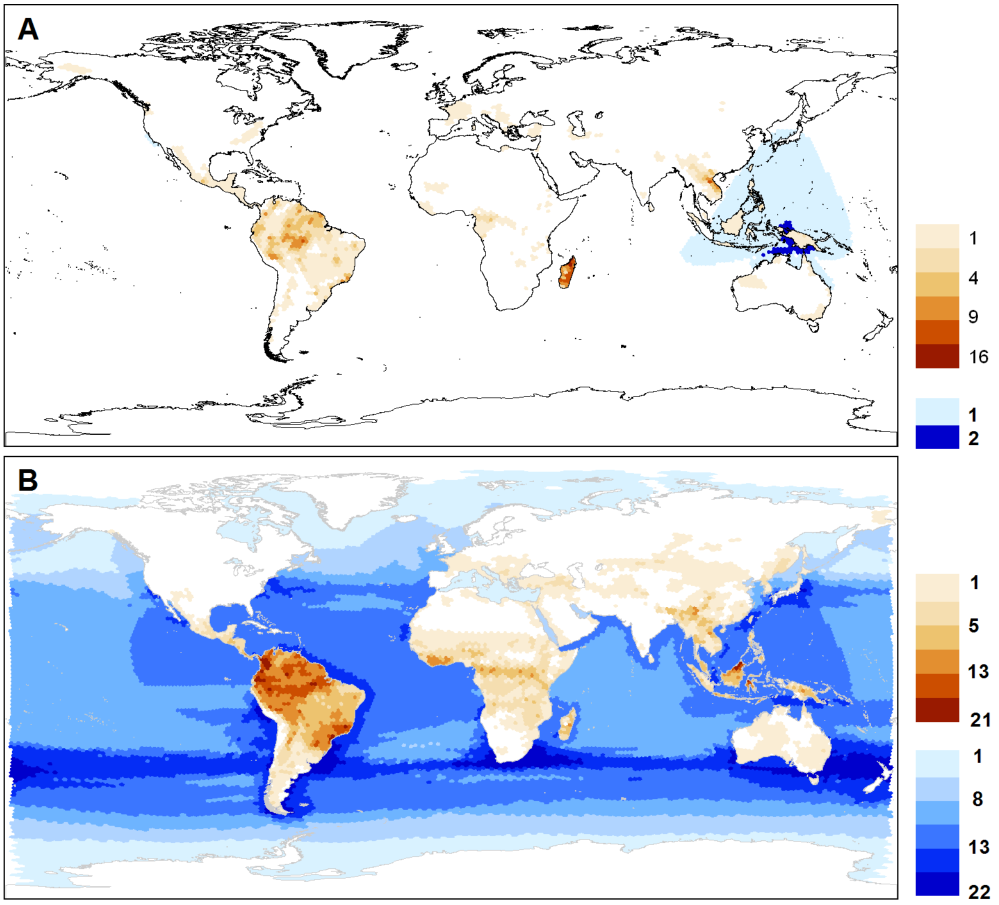


Figure 3. Threat status across mammalian families in relation to overall threat levels across all mammals (dashed line: 26%). Each family (*n*=153) is represented by a dot, indicating the percentage of threatened or extinct species, in relation to the total number of species in the family for which the threat status is known (i.e. excluding Data Deficient, DD, species) Colored bands indicate significance levels (one-tailed binomial test). Families 1 to 25 are those for which threat levels are highly significantly (p <0.01) different from expected (between brackets: number of threatened or extinct species/number of non-DD species).



1	Tapiridae, Perissodactyla (4/4)
1	Hippopotamidae, Cetartiodactyla (4/4)
2	Tarsiidae, Primates (5/6)
3	Ursidae, Carnivora (6/8)
4	Potoroidae, Diprodontia (7/11)
5	Suidae, Cetartiodactyla (10/17)
6	Chrysochloridae, Afrosoricida (10/18)
7	Hominidae, Primates (6/6)
7	Nesophontidae, Eulipotyphla (6/6)
8	Moschidae, Cetartiodactyla (7/7)
9	Hylobatidae, Primates (16/16)
10	Indriidae, Primates (12/13)
11	Capromyidae, Rodentia (17/19)
12	Lemuridae, Primates (16/19)
13	Atelidae, Primates (18/28)
14	Cercopithecidae, Primates (72/120)
15	Cervidae, Cetartiodactyla (26/45)
16	Pteropodidae, Chiroptera (69/165)
17	Bovidae, Cetartiodactyla (54/137)
18	Talpidae, Eulipotyphla (3/36)
19	Dipodidae, Rodentia (4/42)
20	Didelphidae, Didelphimorphia (9/78)
21	Molossidae, Chiroptera (11/80)
22	Phyllostomidae, Chiroptera (19/152)
23	Vespertilionidae, Chiroptera (44/325)
24	Sciuridae, Rodentia (33/238)
25	Cricetidae, Rodentia (110/612)

Figure 4. Global patterns of knowledge, for land (terrestrial and freshwater; brown) and marine (blue) species. A) Number of species newly described since 1992 (land *n*=357; marine *n*=3). B) Data Deficient species (land *n*=777; marine *n*=46).



Chapter One Appendix

Supporting material for “The status of the world’s land and marine mammals: diversity, threat, and knowledge”.

Introduction

For over four decades, IUCN (the International Union for Conservation of Nature, formerly the World Conservation Union), mainly through its Species Survival Commission (SSC), has been assessing the conservation status of species, subspecies, and populations on a global scale in order to highlight taxa at risk of extinction, and thereby promote their conservation. Today, the IUCN remains committed to providing the world with the most objective, scientifically based information on the current status of global biodiversity. IUCN disseminates information on the taxonomy, conservation status and distribution of taxa through the IUCN Red List of Threatened Species^{TM} (www.iucnredlist.org), currently updated on an annual basis.

As part of IUCN’s efforts to rapidly expand the taxonomic coverage of the IUCN Red List, and to provide a core set of supporting documentation to underpin the IUCN Red List assessments (Rodrigues et al. 2006), IUCN, in collaboration with several key partners, pioneered a series of global, comprehensive species assessments that provide an effective method for gathering, synthesizing, reviewing and disseminating the most accurate scientific data available for biodiversity conservation. To date, comprehensive species assessments have been completed for, among others, all of the world’s amphibians (Stuart et al. 2004) and hermatypic reef-building corals (Carpenter et al. 2008). Assessments are ongoing for many other taxa.

The current dataset on mammals is the product of a similar initiative to undertake a global, comprehensive assessment of the conservation status of all mammalian species. Prior to this assessment, the last time all mammals were assessed globally was in 1996 (IUCN 1996), and the majority of those assessments are out-of-date. Although the primary objective of the current initiative was to place each mammal species in a category of threat using the IUCN Red List system (IUCN 2001), the overall product includes a suite of supporting information, incorporating data on distribution, population numbers and trends, habitat, life history, threats, conservation actions, conservation status, and utilization for each individual wild mammal species. The resulting data, covering 5488 species (includind *Homo sapiens*), are the culmination of a systematic collection and documentation process conducted over a period of nearly five years (2003-2008), involving a partnership of numerous institutions, universities and museums, reviewed at 28 workshops, and the participation of more than 1,700 experts.

Data compilation

The assessment process comprised two core components: one centered around consultation with IUCN SSC Specialist Groups and stand-alone Red List Authorities, and another involving peer-review through workshops. The IUCN Species Survival Commission is an established knowledge network of ~8,000 volunteer members working in almost every country of the world. SSC members are deployed in more than 120 Specialist Groups and Task Forces, with some 2,000 members being part of the mammal Specialist Group network. Currently, there are 29 Specialist Groups with a taxonomic focus on mammals, and one stand-alone Red List Authority (Small Nonvolant Mammal Red List Authority). Relative to other taxa, the existing Specialist Group structure for mammals is remarkably strong for certain groups, with many having produced at least one IUCN SSC Action Plan in the last decade. Consequently, in cases where species were within the jurisdiction of well-coordinated groups, they were, as far as possible, assessed and reviewed by the members of these groups (as part of core Specialist Group activities).

In contrast, the SSC network is somewhat less developed with regard to small mammals, given that these contribute the overwhelming diversity of species (for example, more than one-half of all mammals are rodents). In such cases, we employed a workshop methodology, to provide a platform for discussion, interaction, and group peer-review of species relationships, life-history data and distribution maps. Workshops have proven to be most productive in terms of collating the greatest amount of species-based information within a relatively short time period. For the purpose of conducting careful detailed review of all mammal assessments, we conducted a series of 28 workshops in 18 countries around the world (and usually in collaboration with existing Specialist Groups):

1. Africa (Small Mammals) - January 24–30, 2004 (United Kingdom)
2. South Asia (Non-volant Small Mammals) - February 9-15, 2004 (India)
3. Southeast Asia (initial assessment workshop) - May 3-7, 2004 (Thailand)
4. Africa (Small Mammals, maps only) - August 22-26, 2004 (United Kingdom)
5. Philippines (initial assessment workshop) - November 2-3, 2004 (United States)
6. Edentates – December 17-18, 2004 (Brazil)
7. African Primates – January 26-30, 2005 (United States)
8. Madagascar – April 4-8, 2005 (Madagascar)
9. Sirenia – August 1, 2005 (Japan)
10. Japan – August 6-8, 2005 (Japan)
11. Australia/Pacific – August 15-19, 2005 (Australia)
12. Brazil and Guyanas – October 16-19, 2005 (Brazil)
13. Mongolia – October 31 - November 4, 2005 (Mongolia)
14. Southwest Asia – November 22-25, 2005 (Turkey)
15. Andes (Small Mammals) – February 6-10, 2006 (Colombia)
16. Asian Squirrels – March 27-29, 2006 (India)
17. Philippines – April 9-10, 2006 (Philippines)
18. Southeast Asia (Large Mammals and Bats) – May 2-6, 2006 (Indonesia)
19. Southeast Asia (Rodents) – May 2-5, 2006 (United States)
20. Europe – May 18-22, 2006 (Austria)
21. Old World small Carnivores – July 3-7, 2006 (Vietnam)
22. Asian Primates – September 7-12, 2006 (Cambodia)
23. Cetaceans – January 22-26, 2007 (United States)
24. Southern Cone – October 8-12, 2006 (Brazil)
25. Cats – September 21-22, 2007 (United Kingdom)
26. Mediterranean Mammals – October 9 – November 2, 2007 (Spain)
27. Neotropical Primates – November 28 - December 02, 2007 (United States)
28. Mesoamerica and the Caribbean (Small Mammals) – January 25-30, 2008 (Honduras)

Prior to the workshops, data were collected by teams of researchers who relied on the available literature to document the current state of knowledge. In some cases, enormous amounts of information are available, but in the case of most species very little is known even about the basic ecology of a species in the literature. The documentation in the species accounts reflects this inequality.

During each workshop, invited species experts (including persons with both taxonomic knowledge as well as knowledge of threats "on the ground") were brought together to: 1) build consensus on the state of knowledge of the species; 2) fill in the knowledge gaps with both published and unpublished data; and 3) review maps of species distribution. Once complete, and under the guidance of facilitators trained in the use of the 2001 IUCN Red List Categories and Criteria (IUCN 2001), experts evaluated each species against a variety of thresholds for geographic range size, population size and rates of population reduction to make an assessment of extinction risk. Following each workshop, the entire set of supporting documentation was subject to final checks, while all IUCN Red List assessments were evaluated against the supporting data during a series of consistency checks (to ensure both the proper use of the categories and criteria and that supporting evidence was provided accordingly).

Type of data collected

For the first time, comprehensive, peer-reviewed data on the distribution, abundance, population trends, ecology, habitat preferences, threats, conservation status, utilization, and conservation actions for all 5487 currently recognized wild mammal species are available. Each species has also been coded according to the IUCN Habitats and Threats Classification Schemes, making it possible to analyze, for example, their habitat preferences and major threats. More specifically, the following data were collected on each species:

Systematics

For each species, data were was collected on species, genus, family, order, taxonomic authority, commonly used synonyms, English and other common names (if any), and taxonomic notes (if needed, normally used to clarify difficult or confusing issues).

We used the 3rd edition of *Mammal Species of the World – A Taxonomic and Geographic Reference* (Wilson and Reeder 2005) as the taxonomic framework. However, as the text for this authoritative work was effectively completed in 2003, it has been necessary to depart from this standard lexicon in well-justified circumstances. In such cases, and except in very exceptional circumstances, any newly recognized species (either newly described or newly split) or any other proposed taxonomic change had to be published in a peer-reviewed journal or other authoritative taxonomic work (e.g., a major faunistic treatise). As noted later, our classification is current as of December 2007; some recently proposed changes (e.g.,Koepfli et al. 2008, Radespiel et al. 2008) are not accommodated.

Although the IUCN Red List is not intended to be a definitive taxonomic source, it strives to be taxonomically coherent and consistent at all ranks. Our higher-level classification largely follows that of *Mammal Species of the World*, but again deviates in some respects. At the level of Order, for example, the primary deviation is recognition of the Cetartiodactyla, to include the previously recognized orders Cetacea (whales, dolphins and porpoises) and Artiodactyla (bovids, hippos, giraffids, deer and relatives) (e.g., Gatesy et al. 1996, Nikaido et al. 1999, Murphy et al. 2001, Amrine-Madsen et al. 2003, Arnason et al. 2004, Geisler and Uhen 2005). While a case can be made for continuing use of the name Artiodactyla for this clade (Archibald 2003), we have decided to use the now established Cetartiodactyla to avoid confusion.

General information

General text information was compiled on: geographic range; population (usually a qualitative assessment of abundance or rarity in the absence of quantitative information); habitat and ecology (including, in particular, habitat preferences and ability to adapt to anthropogenic disturbance, as well as any particular biological traits that may render a species particularly vulnerable); threats; and conservation actions (in particular noting occurrence in protected areas).

Distribution maps

As part of the minimum supporting documentation for completing an IUCN Red List assessment, we mapped the distributions of each mammal in ESRI shapefile format

(ArcView GIS 3.x and ArcGIS 9.x). The maps take the form of broad polygons that join known locations. A species' distribution map can consist of more than one polygon where there is an obvious discontinuity in suitable habitat. For some range-restricted taxa, we have tried to map distribution ranges with a higher degree of accuracy, sometimes down to the level of individual subpopulations. Individual polygons are coded according to species' presence (e.g., extant, possibly present, extirpated) and origin (e.g., native, reintroduced).

Of the 5,488 mammals for which we undertook an IUCN Red List assessment, we were able to map the ranges of 5,395 species (maps are missing for Extinct species and typically for some Data Deficient species, such as those known from non-specific type localities). These spatial data used the maps collected by W. Sechrest (2003) as a starting point for part of the species, significantly improved in accuracy and detail through expert editing. A list of countries of occurrence is coded, noting whether or not it is native extant, extirpated, introduced or re-introduced.

Habitat preferences

Each species is coded against the IUCN Habitats Classification Scheme (IUCN 2008)

Major Threats

Each species is coded against the IUCN Threats Classification Scheme (IUCN 2008).

Conservation Actions

Each species is coded against the IUCN Conservation Actions Classification Scheme (IUCN 2008).

Utilization

Each species is coded against the IUCN Utilization Classification Scheme (IUCN 2008) (focusing on the purpose/type of use, the primary forms removed from the wild, and the source of specimens in commercial trade). Species that are listed on any of the CITES appendices are also indicated.

2008 IUCN Red List Assessment

Based on the information above, we used the 2001 IUCN Red List Categories and Criteria (Version 3.1) (IUCN 2001), to undertake an assessment of extinction risk for each mammal species. The IUCN Red List Categories and Criteria are the most widely accepted system for classifying extinction risk at the species level (Rodrigues et al. 2006, Butchart et al. 2005, Hoffmann et al. 2008, de Grammont and Cuarón 2006), and as noted above have already been used in several other global assessments to date (Stuart et al. 2004, Carpenter et al. 2008). The IUCN Red List Categories include eight different categories of threat (Fig. S1): Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). A species qualifies for one of the three threatened categories (CR, EN, or VU) by meeting a critical threshold for that category in one of the five different available criteria (A-E). The criteria are designed to be objective, quantitative, repeatable, and to handle uncertainty.

Each IUCN Red List assessment is accompanied by a rationale that explains how it was justified, the reason for any change from previous assessments (i.e., genuine change in species' status, or non-genuine due to new or better information available, incorrect information used previously, taxonomic change affecting the species, previously incorrect application of the IUCN Red List Criteria), the current population trend (i.e., increasing, decreasing, stable, unknown), date of assessment, names of assessors and evaluators, and any notes relating to IUCN Red Listing (e.g., any important issues in deciding the category).

Assessments are done at the species level, integrating the information across all populations and/or subspecies. Threat categories therefore reflect the overall conservation status of the species, which may for example be of Least Concern despite particular populations/sub-species being highly threatened. In some cases subspecies and/or populations are also assessed individually, but these results are not included in the statistics and analyses presented in this paper.

Bibliography

A list of important references used to compile the information for each species assessment was recorded for each species.

Data limitations

Although we consider the current dataset to be the most comprehensive currently available for mammals, covering all known species, there are limitations. In particular, the following should be noted:

Missing species and species coverage

Since mid-1992 (when the second edition of *Mammal Species of the World* was compiled; *26*), 373 new living mammal species were described—a rate of 24+ new descriptions per year (Reeder et al. 2007) (this excludes species discoveries resulting from taxonomic changes). The rate of mammal descriptions remains high, with 61 species described in the years 2006 and 2007 alone. The overall number of species discoveries is much higher: Patterson (1996) found that for every newly described species of Neotropical mammals (in the 1982 -1993 period), three others were rediscovered in Museum drawers and biochemical labs, resurrected from prior synonymy.

Although we have endeavored to trace all recently described species, it is possible one or two may have eluded our attention, especially if published in obscure media. In general, the cut-off date for including species in the present assessment was Dec 31st, 2007; however, a few species described in 2008 (*Rhynchocyon udzungwensis* [*29*], *Miniopterus petersoni* (Goodman et al. 2008), *Cacajao hosomi* and *C. ayresi* (Boubli et al. 2008)) are included. A single species currently in press (*Mico* sp. nov.) has also been included.

It is worth noting that the mammal faunas in some parts of the world remain poorly known, including, for example, the Andes, most of Central Africa and parts of West Africa, Angola, parts of South and Southeast Asia, and Melanesia. In addition, many species' names, especially in the tropics, actually represent complexes of several species that have not yet been resolved. For our purposes, and pending the availability of published information to the contrary, these are treated as single species, until resolution of their taxonomic status is published.

Domestic species (e.g. Dromedary *Camelus dromedarius*; Domestic Goat *Capra hircus*; Domestic Sheep *Ovis aries*) were excluded from this assessment.

Incomplete ranges

Because of the conservative approach taken in mapping species, the ranges for many are likely to be minimum estimates of the limits of species' distributions. A rule was followed allowing interpolation of occurrence between known localities if the ecological conditions seemed appropriate, but not permitting extrapolation beyond known localities. In other words, to the best of our knowledge, maps represent current known limits within historical native range (any introductions are coded accordingly, and are excluded for the purposes of analysis), with the obvious caveat that species occurrence is not homogeneous within the polygon. Some species are therefore almost certain to occur more widely than mapped. Because of this, some regions are recorded as having lower mammal diversity than may eventually prove to be the case. On the other hand, species' ranges were mapped as generalised polygons which often include areas of unsuitable habitat, and therefore species may not occur in all of the areas where they are mapped.

Threats

The information on the relative importance of different threatening processes to mammal species is incomplete. We coded all threats that appear to have an important impact, but not their relative importance for each species.

Data Deficient species

A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. A taxon in this category may be well studied, and its biology well known, but appropriate data on abundance and/or distribution are lacking. Data Deficient is therefore not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that threatened classification is appropriate (IUCN 2001).

The percentage of species assessed as Data Deficient (15%) is higher than previously indicated for mammals (7.8%) (Baille et al. 2004). There are three likely explanations for this. The first has to do with the large number of recently described species for which it is difficult to discern the real taxonomic and distributional limits of the taxa being assessed. This is particularly the case for many of the recently described lemurs in Madagascar, where 42 were assessed as Data Deficient. The second explanation is due to a number of species formerly erroneously listed as Least Concern moving to the category Data Deficient, particularly in the New World. The third is simply due to lack of knowledge that permits a reliable assessment. Because many Data Deficient species are likely to have small distributions or populations, or both, they are intrinsically likely to be threatened. Consequently, in accordance with IUCN guidelines, species assessed as Data Deficient should not be considered as "not threatened". With further survey work and the availability of improved information, it is anticipated that many of these species, if indeed proven to be valid taxa, will be reassessed. This is a deliberate precautionary approach in accordance with the IUCN guidelines.

Data Analysis

A subset of those data collected, both tabular and spatial, was used in the present analyses.

Tabular data

The analyzed data included tabular information for 5487 species. These correspond to all evaluated, excluding *Homo sapiens*.

- Taxonomy: allocation of each species to genus, family and order.

- Conservation status: each species was classified under one of the IUCN Red List Categories – Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered (including Critically Endangered – Possibly Extinct), Extinct, Extinct in the Wild and Data Deficient.

- Population trends: current known or inferred trends of each species' overall population, described as *increasing*, *decreasing*, *stable*, or *unknown*.

- Threats: mechanisms in which species populations are negatively affected, including both those driven directly by human activities (e.g., habitat loss, pollution) and those that correspond to natural processes (which may be magnified by human activities; e.g., diseases). In these analyses we considered the following main threat types: *habitat loss and degradation, harvesting, pollution, accidental mortality, diseases* and *invasives* (IUCN 2008). Note that a species may be not threatened (*sensu* IUCN Red List, i.e. not categorized as Vulnerable, Endangered or Critically Endangered) and still be affected by a particular threat. Throughout, we consistently refer to the former as 'threatened species' and to the latter as 'species affected by threat X'. Also note that for a species to be listed as affected by a particular threat it has to be negatively affected (or potentially affected); for example, species codded as affected by 'harvesting' are not all of those for which harvested as been recorded, but those for which harvesting has a negative effect.

- Date of description: the date when a taxon was first recognized as unique (either as a species or as a subspecies). A species' date of *description* is often not equivalent to the date of *discovery*. The overall number of species recognized increases over time as a result of both new species descriptions and taxonomic changes elevating previously described taxa to the species level.

These data represent only a subset of the information collected for each species as part of the IUCN Red List assessments (see Section 1).

Spatial data

Distribution maps were available for 5395 species. This is a subset of those species for which tabular data were available, excluding 76 Extinct, two Extinct in the Wild, and 14 Data Deficient species and for which the range is insufficiently known. Species were

mapped as generalized polygons of plausible range, encompassing areas of known current presence. For the present analyses, only those polygons where the species was both reported as native (or possibly native, including reintroduced) and currently present (or possibly present) were included, thus excluding historical and introduced ranges.
As described above, species' range maps are coarse generalizations of their distributions, generally obtained as 'envelopes' including original records (point data) and through interpolation (using, for example, habitat information) from original records. They may include relatively extensive areas from which the species is absent (e.g., terrestrial habitats within a freshwater species' range) and are therefore likely to overestimate the species' true area of occupancy (Hulbert and Jetz 1007). Nonetheless, at the coarse scale of the present analyses (spatial units ~ 22,300 km^2, see below) this bias is not expected to significantly affect the global spatial patterns found (Hulbert and Jetz 1007).

For poorly known species, particularly those considered Data Deficient and known from only a few records, the mapped range may underestimate the true distribution.
Most species' ranges were either wholly in land (including freshwater and volant species) or in the sea, but seven species were mapped across both. These include, for example, the West African Manatee (*Trichechus senegalensis*) that occupies coastal marine, estuarine, and freshwater habitats in West Africa, using coastal areas as far as 75 km offshore (Powell 1990) and rivers as far as 2000 km inland (Kienta 1985). For these 'cross-realm' species, their ranges were split into marine and land sections (using the coastline as the boundary) and analyzed separately (see below). Overall, 5282 species were maped as land mammals and 120 species were mapped as marine mamals, with seven species in common between both lists.

The separation between land and marine species was purely based on their mapped ranges, not on the habitats that they use. As a result, some that use marine habitats were mapped completely in land. These include freshwater and/or estuarine species that occupy a marine area that is too narrow to map, for example: Eurasian Otter (*Lutra lutra*), which in some parts of its range forages within a few hundred meters offshore

(Kruuk 1995); Water Rat (*Hydromys chrysogaster*), a mainly freshwater and brackish water species that also uses coastal mangroves (Flannery 1995).

Analytical Methods

Spatial units

Data were analyzed using a geodesic discrete global grid system, defined on an icosahedron and projected to the sphere using the inverse Icosahedral Snyder Equal Area (ISEA) Projection (Sahr et al. 2003). This corresponds to a hexagonal grid composed of individual units (cells) that retain their shape and area (~22,300 km^2) throughout the globe. These are more suitable for a range of ecological applications than the most commonly used rectangular grids (Birch et al. 2007). A row of cells near latitude 180°E/W was excluded (Fig. S2) as these interfered with the spatial analyses. This creates an artificial narrow band of no data around all maps (Fig. 1, 2, 4).

The range of each species was converted to the hexagonal grid for analysis purposes, with land and marine cells (and their species) analyzed separately. Coastal cells were clipped to the coastline into land and marine sections. The ranges of 'cross-realm' species were also clipped to the coastline into land and marine sections, and analyzed accordingly with land and marine cells.

The maps created in each analysis (Fig. 1, 2, 4) have patterns for marine species mapped on a blue scale, and patterns for land species mapped on a brown scale. Different numerical scales are used for land and marine, as the numbers of species differ by more than an order of magnitude.

Species richness

Patterns of species richness (Fig. 1A) were mapped by counting the number of species in each cell (or cell section, for species with a coastal distribution). Information on the percentage of species in tropical and subtropical moist broadleaf forests was obtained using the biome coverage by Olson and colleagues (2001).

Phylogenetic diversity

We created a phylogenetic tree encompassing all analyzed species based on a recently published mammalian super tree (Bininda-Emonds et al. 2007). The original phylogeny comprised 4510 species. Of these, 4506 were matched to a species in the current assessment (3909 matched directly; 597 matched to a synonym); the unmatched four were either extinct prior to 1500, or domestic. One hundred and fifty-five species were deleted from the original tree: 138 corresponding to taxa no longer recognized as separate species (lumped to another species already on the tree); four for which no match was found; 12 that are Extinct or Extinct in the Wild; and *Homo sapiens*. Deleting this set of species from the tree was done by removing all unique branches associated with it.
The resulting sub-tree had 4355 species. This was expanded to include all extant species assessed by adding 1054 extra species. Those were added to the tree using information on their taxonomy to infer their relative phylogenetic position. The following rules were adopted when adding a new species to the tree:

- For species that were added to existing polytypic genera (946 species), each was added as a split at the basal branch for the corresponding genera (i.e. the last branch common to all species in a given genus).

- For species that were added to existing monotypic genera (81 species), the monotypic genus was split into two species, with the position of the split given by the average split position of polytypic genera in the same family. In families composed of monotypic genera only, the position was given by the average split position of polytypic genera in the same order. In one case where the order had only monotypic genera, the position was given by the average split position of polytypic genera across all mammals.

- For species that corresponded to new genera (26 species), a new branch was added at the basal branch for the corresponding family.

- For one species that corresponded to a new family, a new branch was added at the basal branch for the corresponding order.

The final phylogenetic tree comprised 5409 species, which includes all 5395 species for which distribution maps were available. The phylogenetic diversity of a given site is a measure of species diversity that accounts for the phylogenetic relationship between species (Faith 1992). It is calculated as the sum total of the branch lengths for the sub-tree representing all species at the site (Fig. S3A; Faith 1992, Faith 1994, Rodrigues and Gaston 2002). Given two sites with the same number of species, the phylogenetic diversity is higher when species are less related (Fig. S3B) than when they are clustered in the taxonomic tree (Fig. S3C). The phylogenetic diversity of a site is therefore not a measure of the phylogenetic uniqueness of the site's fauna, but a measure of the overall evolutionary history encompassed by all species at the site. The phylogenetic diversity of each cell was mapped for land and marine species (Fig. 1B).

Restricted-range species

Restricted-range species were defined as those 25% of species with the smallest range sizes (Stattersfield et al. 1998, Orme et al. 2005, Grenyer et al. 2006). Range sizes were calculated in GIS, directly from the species' polygons on an equal-area projection. Restricted-range species were defined separately for land (n=1321) and for marine (*n*=30) species. For cross-realm species, the value used was that of the entire range (not just the land or marine sections). Richness in restricted-range species was mapped to identify areas that are global centers of endemism for land and marine species (Fig. 1C).

Median range size

The spatial pattern of variation in species' range sizes was investigated by calculating, for each cell, the median area of the range of all species present (Fig. 1D). A similar approach was applied to birds in previous studies (Hawkins and Diniz-Filho 2006, Orme et al. 2006). For cross-realm species, the range size was that of the entire range (not just the land or marine sections).

Threat levels

Threat levels (percentage of threatened species within a group) cannot be determined exactly given that for Data Deficient species the threat status could not be determined.

Threat levels are therefore presented as an estimated mid-point, and a range between a lower bound and an upper bound. These are defined as:

- Mid-point: percentage of threatened species amongst those for which threat status could be determined (number of threatened species divided by the number of non-Data Deficient species). This corresponds to the assumption that Data Deficient species have the same fraction of threatened species as the other species.

- Lower bound: percentage of threatened species amongst all species assessed (number of threatened species divided by the total number of species assessed). This corresponds to the assumption that none of the Data Deficient species are threatened.

- Upper bound: percentage of threatened or Data Deficient species amongst those assessed (number of threatened or Data Deficient species divided by the total number of species assessed). This corresponds to the assumption that all of the Data Deficient species are threatened.

Threat levels obtained in the 2008 Red List Assessment are not directly comparable with those from 1996 (IUCN 1996), because the categories and criteria employed to allocate species to threat classes have changed (Mace et al. 2008), and because more than 850 new species have since been described or revalidated.

The number of threatened species in each cell was mapped (Fig. 2A) by counting the number of species in IUCN Categories Vulnerable, Endangered or Critically Endangered. The number of species affected by habitat loss and degradation (Fig. 2B), harvesting (Fig. 2C), accidental mortality (Fig. 2D) and pollution (Fig. 2E) was obtained by counting those species in each cell that are affected by such a threat. As described above, these species are not necessarily threatened, and a species may be affected by more than one threat. These four threat categories were chosen to be mapped as they include the two main threats for land species (habitat loss, harvesting) and the two main threats for marine species (accidental mortality, pollution). Note that harvesting does not include direct persecution (e.g. for pest control) or accidental mortality (e.g. fisheries by-catch), which are coded separately. Pollution includes noise pollution and global warming (IUCN 2008). Given that no information has been compiled on which threats are most important for each species, we use the number of species affected by each threat as a measure of the relative importance of different threats.

One-tailed binomial tests were used to investigate which mammalian families have higher or lower than expected percentages of threatened or extinct species (Figure 3). Three families (Neobalaenidae, Notoryctidae and Odobenidae) are not represented in Figure 3 because all of their species are Data Deficient. Care is needed in interpreting these results. That a given family has a significantly lower proportion of threatened or extinct species than the average across mammals does not necessarily mean that it is at low risk of threat in absolute terms. Species extinctions are relatively rare events in geological time (Pimm et al. 1995), and therefore most taxa are highly threatened in relation to what would be expected in the absence of human activities.

Knowledge

The number of species that have been described since 1992 was obtained as the difference between the date of species included in the current assessment and those recognized in the second edition of *Mammal Species of the World* (Wilson and Reeder 1993) (with a cut off date of July 1992 for the inclusion of species). The number of newly described species in the 1992-2008 period has been obtained from the original year of description. The ranges of newly described species were mapped to illustrate areas where new knowledge of mammalian diversity has recently emerged (Fig. 4A). The number of Data Deficient species per cell has been mapped to illustrate areas in need of future research (Fig. 4B).

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Table S1: Number of species in each IUCN Red List Category (EX – Extinct; EW – Extinct in the Wild; CR – Critically Endangered; VU – Vulnerable; EN – Endangered; LC – Least Concern; DD – Data Deficient) for all mammals and for those in each order (grey rows) and each family. For each order or family, we present the significance level from a binomial test comparing the corresponding percentage of threatened or extinct species (amongst non-DD species) with the overall percentage across all species (26%; Figure 3).

FAMILY	**EX**	**EW**	**Subtotal extinct**	**CR**	**EN**	**VU**	**Subtotal threatened**	**NT**	**LC**	**DD**	**Total assessed**
ALL MAMMALS	79	2	81	188	448	505	1141	323	3109	835	**5489**
MONOTREMATA (ns)											
Ornithorhynchidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Tachyglossidae (ns)	0	0	0	3	0	0	3	0	1	0	**4**
Total Monotremata	**0**	**0**	**0**	**3**	**0**	**0**	**3**	**0**	**2**	**0**	**5**
DIDELPHIMORPHIA [&&]											
Didelphidae[&&]	1	0	1	1	0	7	8	2	67	17	**95**
PAUCITUBERCULATA (ns)											
Caenolestidae (ns)	0	0	0	0	0	2	2	2	2	0	**6**
MICROBIOTHERIA (ns)											
Microbiotheriidae (ns)	0	0	0	0	0	0	0	1	0	0	**1**
NOTORYCTEMORPHIA [2]											
Notoryctidae[2]	0	0	0	0	0	0	0	0	0	2	**2**
DASYUROMORPHIA (ns)											
Dasyuridae[&]	0	0	0	1	5	5	11	10	47	4	**72**
Myrmecobiidae (ns)	0	0	0	0	1	0	1	0	0	0	**1**
Thylacinidae (ns)	1	0	1	0	0	0	0	0	0	0	**1**
Total Dasyurmorphia	**1**	**0**	**1**	**1**	**6**	**5**	**12**	**10**	**47**	**4**	**74**
PERAMELEMORPHIA *											
Chaeropodidae (ns)	1	0	1	0	0	0	0	0	0	0	**1**
Peramelidae (ns)	1	0	1	0	4	1	5	1	9	3	**19**
Thylacomyidae (ns)	1	0	1	0	0	1	1	0	0	0	**2**
Total Peramelemorphia	**3**	**0**	**3**	**0**	**4**	**2**	**6**	**1**	**9**	**3**	**22**

FAMILY	EX	EW	Subtotal extinct	CR	EN	VU	Subtotal threatened	NT	LC	DD	Total assessed
DIPROTODONTIA **											
Acrobatidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Burramyidae (ns)	0	0	0	1	0	0	1	0	4	0	**5**
Hypsiprymnodontidae(ns)	0	0	0	0	0	0	0	0	1	0	**1**
Macropodidae*	4	0	4	5	8	9	22	10	30	1	**67**
Petauridae (ns)	0	0	0	1	3	0	4	0	7	0	**11**
Phalangeridae (ns)	0	0	0	4	2	4	10	1	14	1	**26**
Phascolarctidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Potoroidae**	3	0	3	2	2	0	4	2	2	0	**11**
Pseudocheiridae (ns)	0	0	0	0	0	3	3	3	12	0	**18**
Tarsipedidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Vombatidae (ns)	0	0	0	1	0	0	1	0	2	0	**3**
Total Diprotodontia	**7**	**0**	**7**	**14**	**15**	**16**	**45**	**16**	**76**	**2**	**146**
TUBULIDENTATA (ns)											
Orycteropodidae (ns)	0	0	0	0	0	0	0	**0**	1	0	1
SIRENIA **											
Dugongidae (ns)	1	0	1	0	0	1	1	0	0	0	**2**
Trichechidae*	0	0	0	0	0	3	3	0	0	0	**3**
Total Sirenia	**1**	**0**	**1**	**0**	**0**	**4**	**4**	**0**	**0**	**0**	**5**
AFROSORICIDA (ns)											
Chrysochloridae**	0	0	0	1	4	5	10	2	6	3	**21**
Tenrecidae (ns)	0	0	0	0	3	4	7	1	24	1	**33**
Total Afrosoricida	**0**	**0**	**0**	**1**	**7**	**9**	**17**	**3**	**30**	**4**	**54**
MACROSCELIDEA (ns)											
Macroscelididae (ns)	0	0	0	0	1	2	3	1	9	3	**16**
HYRACOIDEA (ns)											
Procaviidae (ns)	0	0	0	0	0	0	0	0	5	0	**5**
PROBOSCIDEA (ns)											
Elephantidae (ns)	0	0	0	0	1	0	1	1	0	0	**2**
CINGULATA (ns)											
Dasypodidae (ns)	0	0	0	0	0	4	4	5	9	3	**21**

FAMILY	**EX**	**EW**	**Subtotal extinct**	**CR**	**EN**	**VU**	**Subtotal threatened**	**NT**	**LC**	**DD**	**Total assessed**
PILOSA (ns)											
Bradypodidae (ns)	0	0	0	1	1	0	2	0	2	0	**4**
Cyclopedidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Megalonychidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Myrmecophagidae (ns)	0	0	0	0	0	0	0	1	2	0	**3**
Total Pilosa	**0**	**0**	**0**	**1**	**1**	**0**	**2**	**1**	**7**	**0**	**10**
SCANDENTIA (ns)											
Ptilocercidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Tupaiidae (ns)	0	0	0	0	2	0	2	0	14	3	**19**
Total Scandentia	**0**	**0**	**0**	**0**	**2**	**0**	**2**	**0**	**15**	**3**	**20**
DERMOPTERA (ns)											
Cynocephalidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
PRIMATES ***											
Aotidae (ns)	0	0	0	0	0	4	4	0	5	2	**11**
Atelidae***	0	0	0	5	8	5	18	0	10	0	**28**
Callitrichidae (ns)	0	0	0	2	6	6	14	2	20	6	**42**
Cebidae (ns)	0	0	0	3	1	2	6	2	9	0	**17**
Cercopithecidae***	0	0	0	12	29	31	72	11	37	2	**122**
Cheirogaleidae (ns)	0	0	0	0	4	2	6	1	7	15	**29**
Daubentoniidae (ns)	0	0	0	0	0	0	0	1	0	0	**1**
Galagidae[&]	0	0	0	1	0	0	1	1	15	1	**18**
Hominidae***	0	0	0	2	4	0	6	0	0	0	**6**
Hylobatidae***	0	0	0	4	11	1	16	0	0	0	**16**
Indriidae***	0	0	0	2	8	2	12	0	1	5	**18**
Lemuridae***	0	0	0	3	4	9	16	3	0	1	**20**
Lepilemuridae*	0	0	0	1	1	1	3	0	0	21	**24**
Lorisidae*	0	0	0	0	2	4	6	0	4	0	**10**
Palaeopropithecidae (ns)	1	0	1	0	0	0	0	0	0	0	**1**
Pitheciidae*	1	0	1	2	6	8	16	1	24	1	**43**
Tarsiidae**	0	0	0	0	2	3	5	1	0	2	**8**
Total Primates	**2**	**0**	**2**	**37**	**86**	**78**	**201**	**23**	**132**	**56**	**414**

FAMILY	EX	EW	Subtotal extinct	CR	EN	VU	Subtotal threatened	NT	LC	DD	Total assessed
RODENTIA &&&											
Abrocomidae (ns)	1	0	1	1	0	0	1	0	2	6	**10**
Anomaluridae (ns)	0	0	0	0	0	0	0	0	6	1	**7**
Aplodontiidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Bathyergidae (ns)	0	0	0	0	0	1	1	1	12	1	**15**
Calomyscidae (ns)	0	0	0	0	0	0	0	0	6	2	**8**
Capromyidae***	6	0	6	4	4	3	11	1	1	0	**19**
Castoridae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Caviidae (ns)	0	0	0	1	0	0	1	2	12	3	**18**
Chinchillidae (ns)	1	0	1	2	0	0	2	0	3	1	**7**
Cricetidae&&&	15	0	15	21	31	44	96	34	468	85	**698**
Ctenodactylidae (ns)	0	0	0	0	0	0	0	0	3	2	**5**
Ctenomyidae*	0	0	0	3	6	6	15	5	16	24	**60**
Cuniculidae (ns)	0	0	0	0	0	0	0	1	1	0	**2**
Dasyproctidae (ns)	0	0	0	1	1	1	3	1	6	3	**13**
Diatomyidae (ns)	0	0	0	0	1	0	1	0	0	0	**1**
Dinomyidae (ns)	0	0	0	0	0	1	1	0	0	0	**1**
Dipodidae&&	0	0	0	0	2	2	4	4	34	8	**50**
Echimyidae (ns)	4	0	4	2	7	4	13	0	47	25	**89**
Erethizontidae (ns)	0	0	0	0	0	1	1	0	11	6	**18**
Geomyidae&	0	0	0	3	1	0	4	1	33	1	**39**
Gliridae (ns)	0	0	0	0	0	2	2	1	15	10	**28**
Heteromyidae (ns)	0	0	0	3	6	5	14	1	46	1	**62**
Hystricidae (ns)	0	0	0	0	0	1	1	0	10	0	**11**
Muridae (ns)	10	0	10	17	62	55	134	24	409	134	**711**
Myocastoridae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Nesomyidae (ns)	0	0	0	1	6	3	10	0	40	9	**59**
Octodontidae (ns)	0	0	0	3	0	2	5	1	5	2	**13**
Pedetidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Petromuridae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Platacanthomyidae (ns)	0	0	0	0	0	1	1	0	1	0	**2**
Sciuridae&&&	0	0	0	2	15	16	33	24	181	41	**279**

FAMILY	**EX**	**EW**	**Subtotal extinct**	**CR**	**EN**	**VU**	**Subtotal threatened**	**NT**	**LC**	**DD**	**Total assessed**
Spalacidae (ns)	0	0	0	0	2	2	4	2	12	3	**21**
Thryonomyidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Total Rodentia	**37**	**0**	**37**	**64**	**144**	**150**	**358**	**103**	**1389**	**368**	**2255**
LAGOMORPHA (ns)											
Leporidae (ns)	0	0	0	1	7	5	13	6	38	5	**62**
Ochotonidae (ns)	0	0	0	1	3	0	4	0	23	3	**30**
Prolagidae (ns)	1	0	1	0	0	0	0	0	0	0	**1**
Total Lagomorpha	**1**	**0**	**1**	**2**	**10**	**5**	**17**	**6**	**61**	**8**	**93**
EULIPOTYPHLA (ns)											
Erinaceidae (ns)	0	0	0	0	2	1	3	0	20	1	**24**
Nesophontidae***	6	0	6	0	0	0	0	0	0	0	**6**
Solenodontidae*	1	0	1	0	2	0	2	0	0	0	**3**
Soricidae (ns)	0	0	0	12	36	28	76	12	217	71	**376**
Talpidae[&&]	0	0	0	0	1	2	3	1	32	5	**41**
Total Eulipotyphla	**7**	**0**	**7**	**12**	**41**	**31**	**84**	**13**	**269**	**77**	**450**
CHIROPTERA [&&&]											
Craseonycteridae (ns)	0	0	0	0	0	1	1	0	0	0	**1**
Emballonuridae[&]	0	0	0	1	2	2	5	1	38	8	**52**
Furipteridae (ns)	0	0	0	0	1	0	1	0	1	0	**2**
Hipposideridae (ns)	0	0	0	1	4	10	15	7	44	18	**84**
Megadermatidae (ns)	0	0	0	0	0	1	1	0	4	0	**5**
Molossidae[&&]	0	0	0	1	2	8	11	2	67	20	**100**
Mormoopidae (ns)	0	0	0	1	0	0	1	0	8	0	**9**
Mystacinidae (ns)	0	0	0	1	0	1	2	0	0	0	**2**
Myzopodidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Natalidae (ns)	0	0	0	2	0	0	2	4	5	0	**11**
Noctilionidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Nycteridae (ns)	0	0	0	0	0	1	1	1	10	4	**16**
Phyllostomidae[&&&]	3	0	3	1	5	12	18	12	121	22	**176**
Pteropodidae***	4	0	4	9	18	38	65	14	82	22	**187**
Rhinolophidae[&]	0	0	0	1	4	5	10	6	47	11	**74**
Rhinopomatidae (ns)	0	0	0	0	0	0	0	0	3	1	**4**

FAMILY	EX	EW	Subtotal extinct	CR	EN	VU	Subtotal threatened	NT	LC	DD	Total assessed
Thyropteridae (ns)	0	0	0	0	0	0	0	0	2	2	**4**
Vespertilionidae&&&	0	0	0	7	17	20	44	30	251	96	**421**
Total Chiroptera	**7**	**0**	**7**	**25**	**53**	**99**	**177**	**77**	**687**	**204**	**1152**
PHOLIDOTA (ns)											
Manidae (ns)	0	0	0	0	2	0	2	4	2	0	**8**
CARNIVORA (ns)											
Ailuridae (ns)	0	0	0	0	0	1	1	0	0	0	**1**
Canidae (ns)	1	0	1	3	3	0	6	4	24	1	**36**
Eupleridae (ns)	1	0	1	0	1	3	4	3	1	0	**9**
Felidae*	0	0	0	1	6	9	16	9	11	0	**36**
Herpestidae&	0	0	0	0	0	3	3	1	27	3	**34**
Hyaenidae (ns)	0	0	0	0	0	0	0	2	2	0	**4**
Mephitidae (ns)	0	0	0	0	0	1	1	0	11	0	**12**
Mustelidae (ns)	1	0	1	0	7	5	12	4	36	6	**59**
Nandiniidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Odobenidae[2]	0	0	0	0	0	0	0	0	0	1	**1**
Otariidae (ns)	1	0	1	0	4	2	6	2	7	0	**16**
Phocidae (ns)	1	0	1	2	1	1	4	0	12	2	**19**
Prionodontidae (ns)	0	0	0	0	0	0	0	0	2	0	**2**
Procyonidae (ns)	0	0	0	1	0	0	1	0	10	3	**14**
Ursidae**	0	0	0	0	1	5	6	0	2	0	**8**
Viverridae (ns)	0	0	0	1	1	9	11	2	17	3	**33**
Total Carnivora	**5**	**0**	**5**	**8**	**24**	**39**	**71**	**27**	**163**	**19**	**285**
PERISSODACTYLA ***											
Equidae*	0	0	0	2	2	1	5	0	2	0	**7**
Rhinocerotidae*	0	0	0	3	0	1	4	1	0	0	**5**
Tapiridae**	0	0	0	0	3	1	4	0	0	0	**4**
Total Perissodactyla	**0**	**0**	**0**	**5**	**5**	**3**	**13**	**1**	**2**	**0**	**16**

FAMILY	**EX**	**EW**	**Subtotal extinct**	**CR**	**EN**	**VU**	**Subtotal threatened**	**NT**	**LC**	**DD**	**Total assessed**
CETARTIODACTYLA ***											
Antilocapridae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Balaenidae (ns)	0	0	0	0	2	0	2	0	2	0	**4**
Balaenopteridae (ns)	0	0	0	0	3	0	3	0	2	3	**8**
Bovidae***	4	1	5	8	20	21	49	16	67	3	**140**
Camelidae (ns)	0	0	0	1	0	0	1	0	2	0	**3**
Cervidae***	1	1	2	1	7	16	24	2	17	10	**55**
Delphinidae (ns)	0	0	0	0	1	2	3	3	13	16	**35**
Eschrichtiidae (ns)	0	0	0	0	0	0	0	0	1	0	**1**
Giraffidae (ns)	0	0	0	0	0	0	0	1	1	0	**2**
Hippopotamidae**	2	0	2	0	1	1	2	0	0	0	**4**
Iniidae (ns)	0	0	0	1	0	1	2	0	0	1	**3**
Monodontidae (ns)	0	0	0	0	0	0	0	2	0	0	**2**
Moschidae***	0	0	0	0	6	1	7	0	0	0	**7**
Neobalaenidae[2]	0	0	0	0	0	0	0	0	0	1	**1**
Phocoenidae (ns)	0	0	0	1	0	1	2	0	2	2	**6**
Physeteridae (ns)	0	0	0	0	0	1	1	0	0	2	**3**
Platanistidae (ns)	0	0	0	0	1	0	1	0	0	0	**1**
Suidae**	0	0	0	2	3	5	10	1	6	1	**18**
Tayassuidae (ns)	0	0	0	0	1	0	1	1	1	1	**4**
Tragulidae (ns)	0	0	0	0	1	0	1	0	6	3	**10**
Ziphiidae (ns)	0	0	0	0	0	0	0	0	2	19	**21**
Total Cetartiodactyla	**7**	**2**	**9**	**14**	**46**	**49**	**109**	**26**	**123**	**62**	**329**

Significantly more threatened than expected: *** p <0.001; ** p < 0.01 * p < 0.5.

Significantly less threatened than expected: $^{\&\&\&}$ p < 0.001; $^{\&\&}$ p < 0.01; $^{\&}$ p < 0.5.

(ns) – non significant; **[1]** all species Extinct; **[2]** all species Data Deficient.

Table S2: Number and percentage of species affected by each of six main threat categories. Species can be affected by more than one threat category; being affected by a threat does not necessarily imply that the species is globally threatened (Vulnerable, Endangered, or Critically Endangered). Land and marine species are those mapped in Fig. 1, and exclude 78 extinct and 14 Data Deficient species; seven species are mapped as both land and marine.

		Threat					
	All assessed/ mapped	**Habitat loss (%)**	**Utilisation (%)**	**Accidental mortality (%)**	**Pollution (%)**	**Invasive species (%)**	**Disease (%)**
All mammals	**5,487**	**2,030 (37)**	**926 (17)**	**284 (5)**	**219 (4)**	**309 (6)**	**117 (2)**
Land mammals	**5,282**	**2,016 (38)**	**872 (17)**	**193 (4)**	**151 (3)**	**306 (6)**	**102 (2)**
Marine mammals	**120**	**2 (2)**	**61 (51)**	**98 (82)**	**75 (63)**	**3 (3)**	**16 (13)**

Figure S1. The IUCN Red List categories. Adapted, with permission, from IUCN (2001).

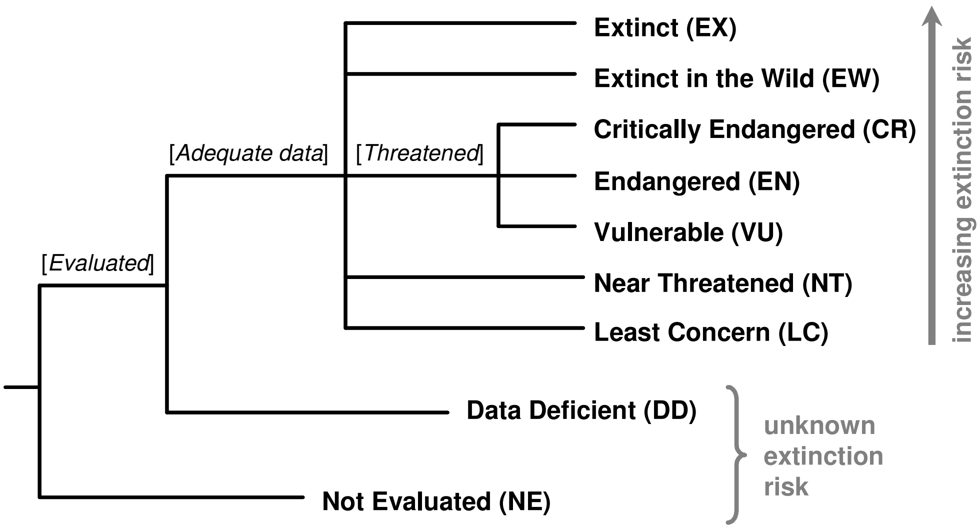


Figure S2. Hexagonal grid used in the spatial analysis: A) viewed on a globe; B) on a cylindrical projection. Cells near 180°E/W were excluded.

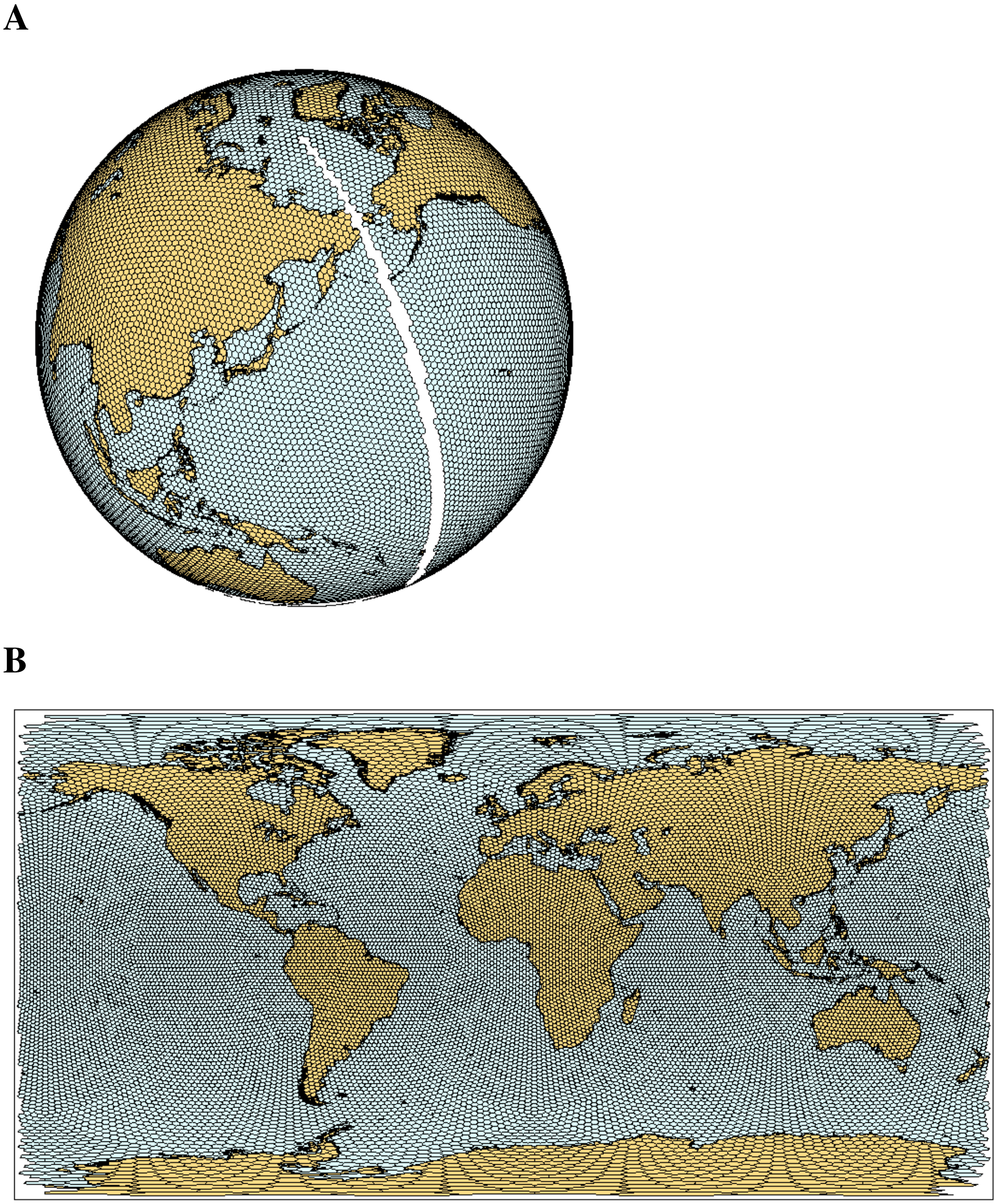
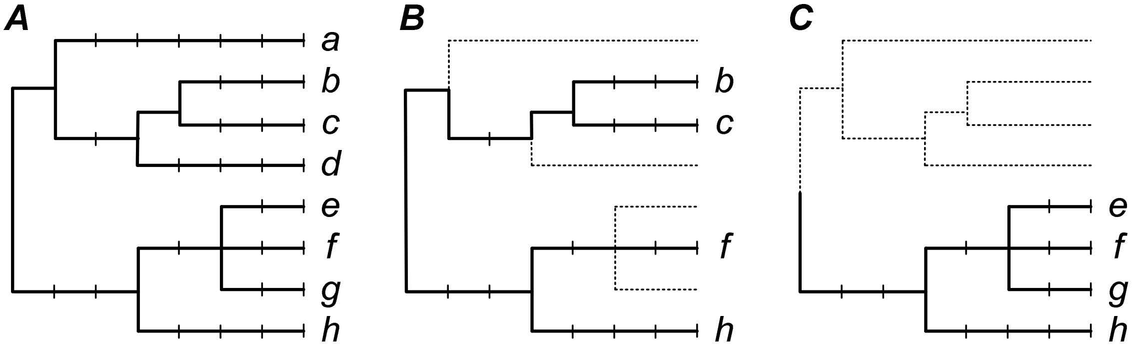


Figure S3. Illustration of the method for calculating the phylogenetic diversity of a set of species. A) Hypothetical phylogenetic tree with eight taxa, *a* to *h*. The length of each branch is given by the number of intervals. The phylogenetic diversity of the tree is the sum of the length of the branches; for all species, phylogenetic diversity = 35. B) Sub-tree for taxa *b*, *c*, *f*, and *h*, with phylogenetic diversity = 21. C) Sub-tree for taxa *e*, *f*, *g*, and *h*, with phylogenetic diversity = 15. Adapted from Rodrigues and Gaston (2002).



Additional analyses not mentioned in the text:

Figure S4. Relationship between latitude and species richness per cell for: A) land species; B) marine species. Northern latitudes positive, southern latitudes negative.

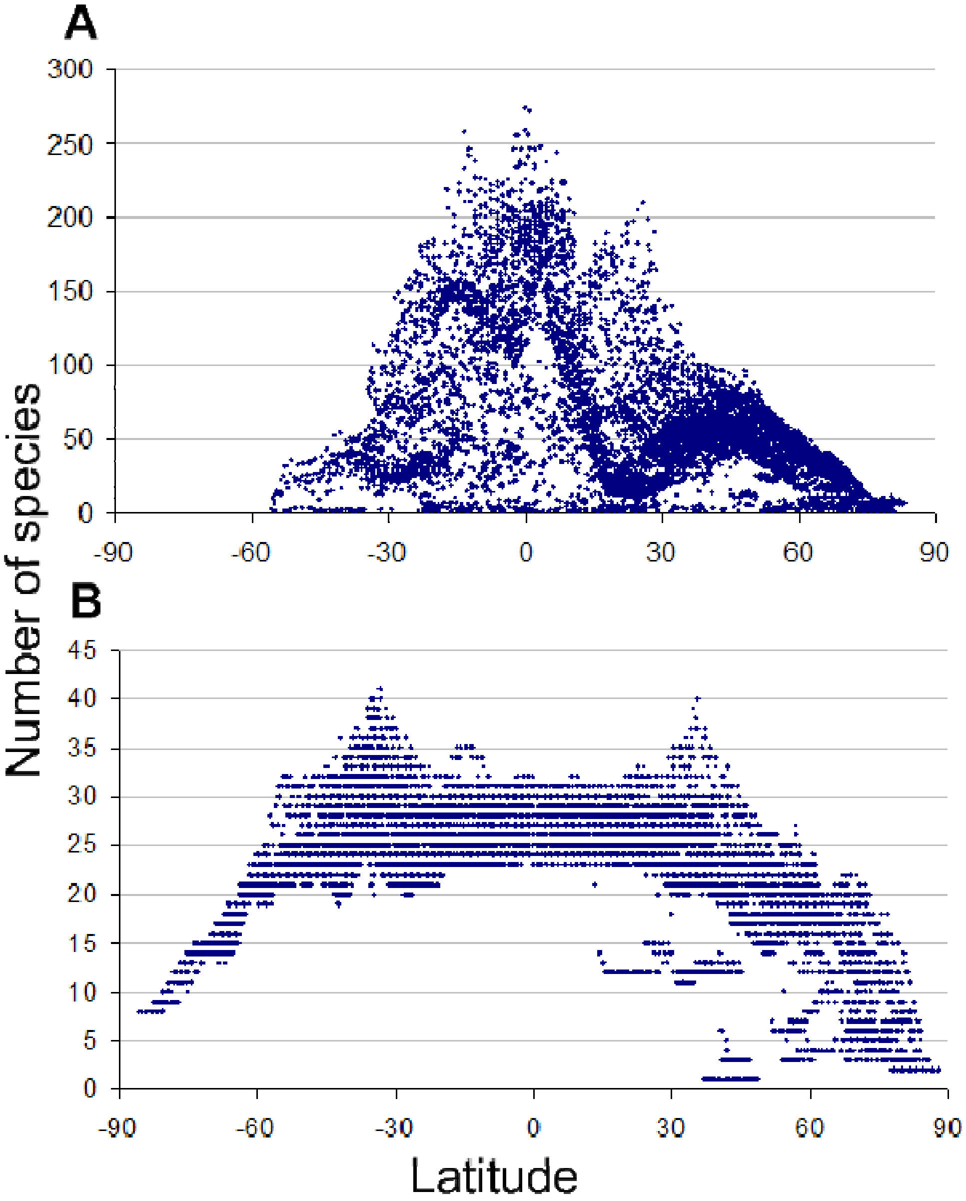


Figure S5. Relationship between species richness and phylogenetic diversity across: A) land species (r^2 =0.98); B) marine species (r^2 = 0.73).

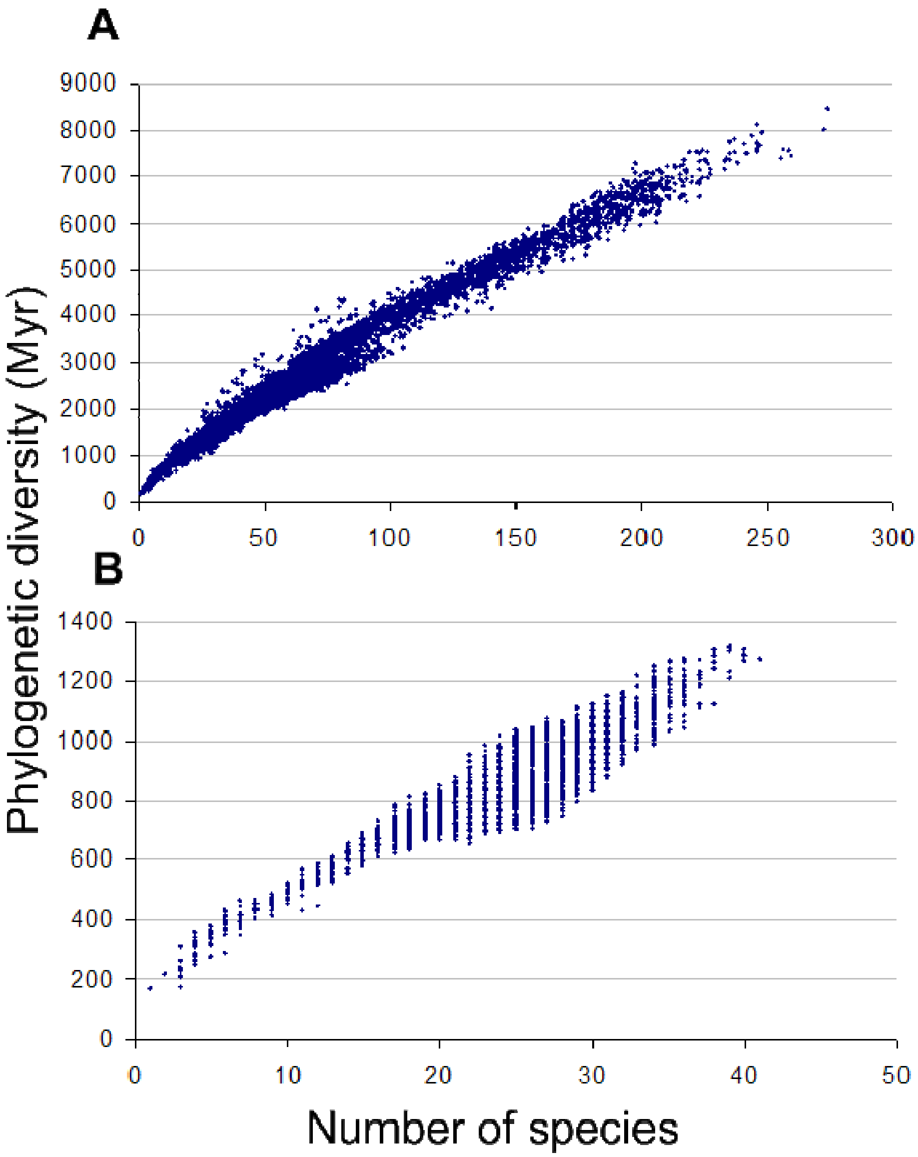


Figure S6. Frequency distribution of range sizes for (A) land mammals (*n*=5282; first quartile ~ 17,700 km^2; median ~ 193.6 km^2; three species range smaller than 1 km^2 are lumped with the first class) and (B) marine mammals (*n*=120; first quartile ~ 3.8 million km^2; median ~ 14.5 million km^2).

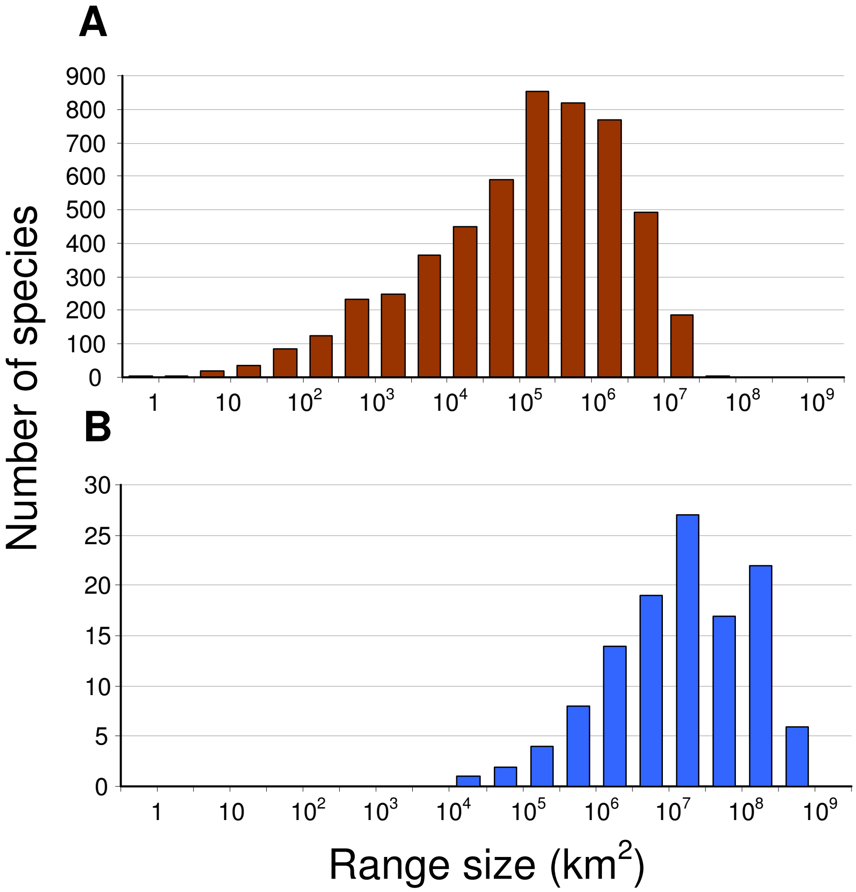


Figure S7. Variation in median range size of species in each cell according to cell latitude, for: A) land mammals and B) marine mammals. Northern latitudes positive, southern latitudes negative.

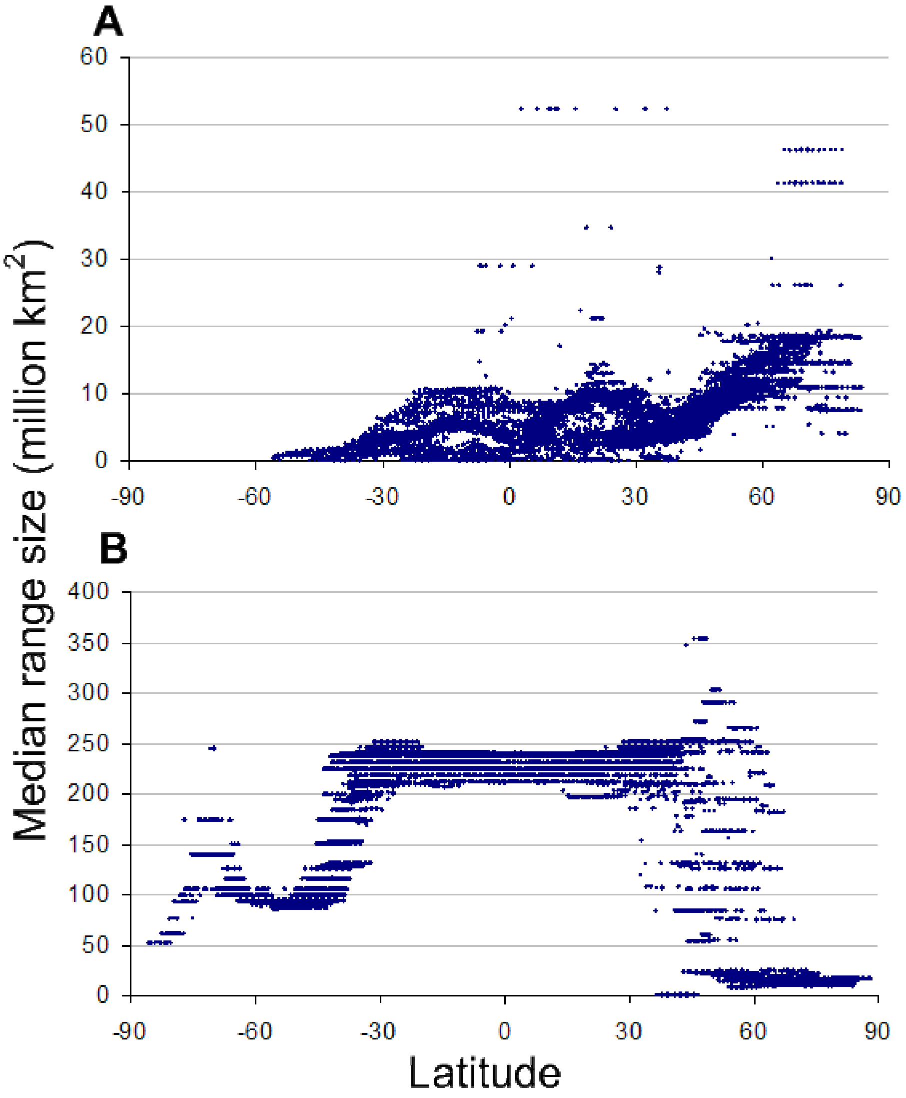
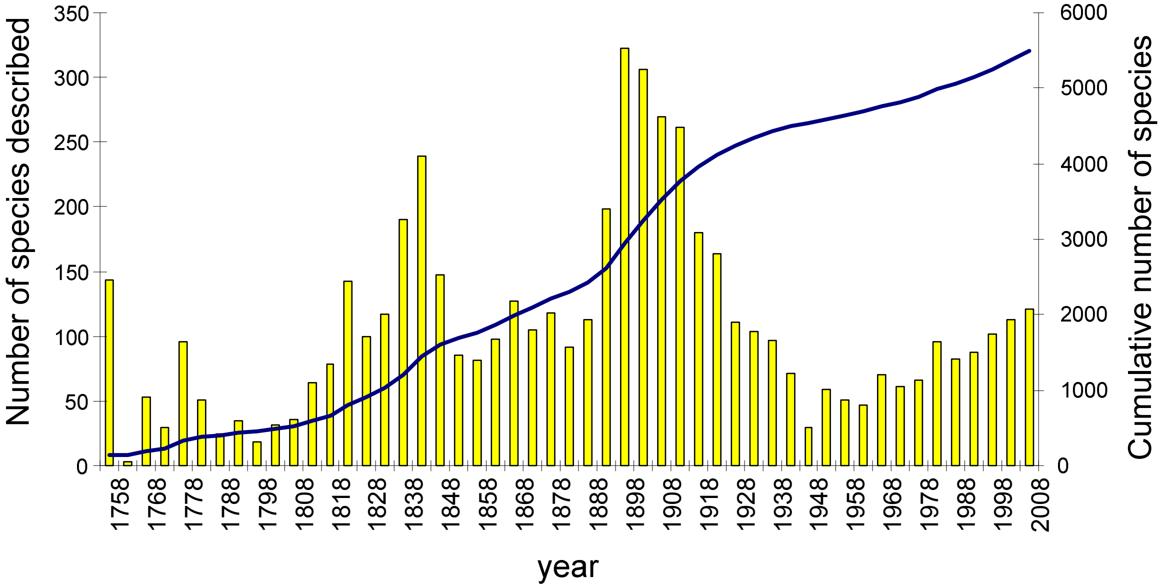


Figure S8. Number of species described per five-year interval (yellow bars) and cumulative total number of species currently recognized as taxonomically valid (blue line) (adapted from ref. *27*). The first column corresponds to all species recognised up to 1758.



Chapter 2

How effective are protected areas at conserving medium- and large-mammal diversity? The case of the Talamanca Mountains, Costa Rica

Abstract

Biodiversity around the world continues to decline despite an increasingly comprehensive network of parks and reserves. Although protected areas are relatively effective at preventing forest loss, their capacity to guard against loss of vertebrates and other species that are hunted, trapped or harvested remains unknown. We use camera traps to collect data on species richness, diversity and relative abundance among protected areas and private properties in lowland and montane tropical forests in Talamanca, Costa Rica. We use these data to evaluate the effectiveness of various stewardship types on the conservation of medium and large mammals in tropical forests. Our data reveal three trends: 1) there is no significant difference between diversity and abundance inside and outside of protected areas in lowland forests, 2) private property retains significantly higher diversity and abundance in montane forests then in lowland forests, and 3) private conservation lands have higher richness, diversity and abundance than the national parks that are designed and maintained specifically for species conservation. We also demonstrate that private properties which enforce existing hunting laws retain more diverse and abundant mammal communities than protected areas generally. We, therefore, conclude that existing protected areas alone are not effectively conserving species that are harvested by hunters and trappers. Without national and international investment in enforcement of existing hunting laws, protected areas will continue to undergo defaunation.

Introduction

Globally, biodiversity continues to decline despite an increasingly comprehensive network of parks and reserves. Although protected areas are useful tools to measure national and international contributions to species conservation (Rodrigues et al. 2004), ecosystem services (Balmford et al. 2002), global biodiversity targets (Chape et al. 2005), and climate change mitigation (Hannah et al. 2007), their ability to prevent species loss has not been well documented. It has been proposed that in the biodiversity-rich tropics, many species would not survive without effective protection (Myers et. al. 2000), however, measuring the contribution of protected areas toward this goal has proven difficult, especially in developing countries. Even the term "protected area" can be deceptive, as in many cases these so-called "paper parks" are designated areas without any enforcement.

Although protected areas are generally considered effective at reducing land clearing (direct habitat loss), they are less effective at mitigating selective logging, hunting and harvesting, fire, and grazing (Bruner et al. 2001). In many cases the forests are still present; however, much of the fauna are missing – especially those medium and large mammals that are targets of hunting (Bodmer 1997, Peres 2001). These so called "empty forests" (Redford 1992) can appear intact even when most of the animals have disappeared, as the direct and indirect effects of defaunation can take many years to show any obvious signs. There is a growing need to develop faunal indicators of effective reserve design and management, especially in tropical forests where animals are difficult to survey and where unregulated hunting could be having a severe impact on species, populations and communities.

Studies of the effectiveness of protected areas have focused on improving management (Hocking 2000) and systematic conservation planning (Green 1996, Margules and Pressey 2000). Although studies have demonstrated the value of protected areas at conserving marine mammals (Reeves 2000), there have been very few studies on their effectiveness at conserving terrestrial mammals, especially those medium and large species most susceptible to hunting pressures. Carrillo et al. (2000), using simple track counts and observations, found that on the Osa Peninsula (Costa Rica) mammals traditionally preferred by hunters were significantly more common inside established protected areas than they were outside. Whereas, this pattern suggests a positive correlation between protection and species occupancy, what is lacking is a more systematic approach that can measure effectiveness in terms of species diversity and relative abundance.

One way of measuring effectiveness of protected areas is to evaluate species diversity both inside and outside designated areas. However, one of the difficulties in measuring species diversity regionally is that species richness and abundance vary naturally along ecological gradients (Brown 2001), especially in tropical montane ecosystems where species community composition varies greatly from lowland tropical forests to montane cloud forests to high elevation grasslands (Lomolino 2001). Mammals present a unique measure of conservation and management success, as they play important roles both maintaining ecosystems and in providing benefits to people (Chapter 1, this thesis). Because mammals are often targeted by hunters, differences in their diversity and abundance inside and outside protected areas would be valuable indicators of their effectiveness at preventing negative human impacts such as hunting.

Given that protected areas have been well documented at reducing habitat loss (Bruner 2001, Andam 2008), the next obvious question is “How effective are protected areas at conserving fauna?” especially those sought after by hunters. However, because of their natural low densities and cryptic and elusive nature, these species are difficult to study and nearly impossible to observe in the wild. This question is difficult to answer for the same reasons tropical mammals are difficult to observe, but advances in survey techniques (e.g. camera traps) now allow us to collect data on species richness, diversity and relative abundance even for elusive species. Medium and large mammals, in particular, are well suited to camera-trap surveys and play very important roles in maintaining biodiversity in tropical forests through herbivory, seed dispersal and predation. With one-quarter of the worlds mammals threatened by habitat loss and hunting (Chapter 1, this thesis), there is an urgent need to understand the impacts of hunting on these mammals in remaining habitats and to understand if protected areas, in fact, offer “protection” to these animals.

A possible confounding factor to using species diversity and abundance as an indicator of the effectiveness of protected areas is that both of these measures change with elevation. Patterns of mammalian diversity vary along both latitudinal and elevational gradients (Stevens 1992, Brown 2001), but are highest in tropical regions with ecological gradients (i.e. elevation) (Chapter 1, this thesis). In fact, using range maps and a literature review, Palminteri et al. (1999) demonstrated that mammal diversity as a whole decreases with elevation in the Talamanca Region of Costa Rica. However, using range maps alone to measure richness and diversity can be deceiving as species are not distributed equally within their known ranges (Rozenzweig 2000), especially in areas that have ecological and anthropogenic gradients. Therefore, while evaluating the effectiveness of protected areas using diversity and abundance as indicators, analysis should take elevation into account.

Camera-trapping has become a widely used non-invasive technique in the survey and assessment of terrestrial large and medium sized mammals (see Cutler and Swan 1999, Kays and Slauson 2008 for reviews). It is less effective for systematically sampling arboreal mammals and birds, as the probability of capture is significantly less due to traditional placement of trap on the ground, and for small (<1kg) mammals as their small heat signatures may not trigger the camera sensor. Remote camera techniques are increasingly useful in determining information on species presence and distribution (Karanth and Nichols 2002, Tobler et al. 2008), abundance (Karanth and Nichols 1998, Carbone et al. 2001), and activity patterns (González-Maya et al. 2009).

In remote wilderness areas, camera-traps are among the few research tools which can be used to survey broad regions. Survey methods such as line transects, track surveys (but see Harvey et al. 2006), and radio-telemetry, which are commonly used in more accessible and open habitats, are not always as effective in dense tropical moist forests where detectability of species and longevity of footprints are very low. However, these methods can be effectively applied in some tropical ecosystems, as Silveira et al. (2003) demonstrated comparable success of these techniques in tropical grassland and shrubland habitats. In closed wet forests, on the other hand, tracks are not retained for more than a few hours, and dense foliage obstructs line of sign of transects and interferes with radio telemetry signals. In closed forests, camera-traps overcome these limitations and can be placed along game trails, water holes, salt licks, and otherwise targeted to capture a variety of information about individuals and species without actively being maintained.

The effectiveness of protected areas in Costa Rica

Costa Rica has been internationally recognized for its extensive national park system which covers approximately 12% of the national territory under some form of formal conservation. An additional 7% of the country is retained in various indigenous territories; however, these lands are offered no formal protection status. Despite its size, the existing network of protected areas is neither representative of the available habitat (Powell et al. 2000) nor is it well connected to allow for movements and flows of species and ecological processes. Costa Rica has also been a leader in developing private wildlife reserves (Langholz et al. 2000) and policy innovations for private forest management (Snider et al. 2003) , such as incentives for conservation for private land owners with ecosystem service payments (Chomitz et al. 1999).

Herein, we present the results of 5 years of field survey work using remote camera-traps to understand patterns of mammal diversity and distribution as a function of elevation and stewardship along both the Caribbean and Pacific flanks of the Talamanca Mountains. We test the hypothesis that protected areas have a positive impact on the populations and communities of medium- and large-mammals. To do so, we use camera-traps to study the distribution and diversity of mammals in lowland and montane forests, both inside and outside of a variety of protected areas, in the Talamanca Mountains of Costa Rica.

Within Costa Rica, the Talamanca Region represents one of the most important habitat and natural forest blocks and the highest level of species endemism in Central America (González-Maya et al. 2008). This region is composed of a mosaic of management types: 55% is national protected areas; 31% indigenous territories; 2% on national wildlife refuges; and, 12% non-protected. The non-protected areas are privately owned and predominantly active and inactive farms (1-10,000 ha), small towns, and tourism and small land holdings. The exceptions are two very large private properties (ACODEFO in the Caribbean lowlands, and Finca Las Alturas in the Pacific highlands) managed exclusively for wildlife conservation. Land use within indigenous territories is mostly a mix of plantain, banana and cacao (Caribbean) (Dahlquist et al. 2007), livestock (Pacific), small mixed crops, agroforestry, and native forests. Hunting and poaching are common on both private lands and in indigenous territories, and illegal commercial and subsistence hunting is becoming increasingly common in the protected areas.

The mammal fauna of Costa Rica has been well described and documented (Wilson 1983, Rodríguez and Chinchilla 1996, Rodríguez et al. 2002, Wainwright 2002). However, the majority of field research, collections, and surveys been concentrated in a handful of locations, namely La Selva Biological Station (Timm et al. 1989, Timm 1994), Monteverde (Timm and LaVal 2000) and more recently the Coto Brus (Pacheco et al. 2006). Harvey et al. (2006) conducted terrestrial mammal surveys in the lowland Caribbean portion of the Talamancas and registered tracks of 27 species, but focused on the indigenous territories and agroforestry habitats rather than intact forests. Large gaps remain in our understanding of the mammal fauna, especially in the mid to high elevations of the Talamanca region where little work has been done. In addition to limited information on large mammals in this area, we know almost nothing about the small mammal fauna and undoubtedly new species still remain undescribed.

Among medium and large mammals, we predict that both alpha and beta diversity will change with elevation. We hypothesize that large and medium sized mammal diversity and abundance will decrease with elevation as fewer and fewer tropical species are able to tolerate the cold climate and even fewer are adapted for the grasslands in the highest portions. However, some temperate specialists only occur in the higher elevations, and thus there is a turnover of species from lowlands to highlands (González-Maya et al. 2008).

Methods

Study Area

This study was conducted in and around the Costa Rican portion of the Talamanca Range-La Amistad Reserves/La Amistad National Park World Heritage Site and includes both the Caribbean (0-3600m) and Pacific (1,000-3600m) flanks of the Cordillera Talamanca (from 8°37´- 9°38´N and 82°24´-83°25´W; total area is approximately 600,000ha) (Fig. 1). The area of inference for the data described roughly follows the remaining forest in the Talamanca Region. Elevations below 1,000m on the Pacific slope were excluded due to lack of remaining native vegetation (González-Maya et al. 2008), and thus the Pacific portion of the study area is relatively small (approximately 12% of study area).

The two flanks of the Talamanca Mountain Range (Cordillera) are remarkably different ecologically, historically, and culturally, considering their proximity to one another. Climate varies dramatically from lowlands to highlands and from Caribbean to Pacific. Caribbean lowlands have daily average temperatures of approximately 26 ˚C and average annual precipitation of 2370 mm with a "mini" dry season in March-April and September-October (Herrera 1985). The Pacific slopes (at 1200m) average 19 ˚C with a marked dry season from December-March. At the highest elevation, on the Chirripó Massif (3820m) temperatures average around 11 ˚C at the summit and rainfall averages 4,000 mm (Chaverri 2008).

At the broadest scale the study area falls within the Talamanca montane forest ecoregion (Powell et al. 2001a), while portions of the lowland Caribbean are within the Central American Atlantic moist forest ecoregion (Powell et al. 2001b). Within the montane portions, at least 30% of the flora are endemic to the ecoregion, including 10,000 vascular and 4,000 non-vascular plants (Powell et al. 2001a). Species are continuing to be discovered in this region, as it is among the least explored regions of Central America (Rodríguez and Monro 2008, Solano 2008, Soto and Monro 2008, Monro 2009, Monro and Rodríguez 2009). In addition, the region is considered an Endemic Bird Area (Stattersfield et al. 1998), is selected among the Global 200 important ecoregions for conservation (Olson and Dinerstein, 2002), and is an important component of the Mesoamerican biodiversity hotspot (Mittermeier et al. 2005).

In 1982 the region was declared a UNESCO-MAB Biosphere Reserve (La Amistad), and in 1983 (1990 extension) the Talamanca Range - La Amistad Reserves/La Amistad National Park was declared a UNESCO World Heritage Site (Kapelle 1996). Within the World Heritage Site, we focused our efforts on La Amistad Biosphere Reserve (and International Peace Park), Chirripó National Park, Hitoy-Cerere Biological Reserve, Las Tablas Protected Zone, and the Talamanca (Bribri) Indigenous Reserve in order to obtain a representative sample of the available land tenures. In addition we sampled in a number of private holdings, protected areas outside the Biosphere Reserve (Cahuita National Park, Gandoca-Manzanillo Wildlife Refuge, La Marta Wildlife Refuge), and indigenous territories (Keköldi) surrounding the World Heritage Site which are important as either buffer zones or as biological corridors (Talamanca-Caribe Biological Corridor).

Over 75% of the study area is currently within a protected area or Indigenous Territory. The majority of the private lands within the study area are located in the Caribbean lowlands, with the notable exception of Finca Las Alturas which retains one of the largest forest blocks below 1500m on the Pacific slopes. All private lands on the Caribbean are below 1000m (most below 500m).

Methods

Camera-trap sampling was conducted using passive sensor 35 mm film and digital camera-traps (PTC technologies, Inc. and Woodland Technologies, both have since gone out of business) for a period of four years (Jan. 2005 - Feb. 2008). Camera-traps were modified to be waterproof and theft-resistant, and outfitted with desiccant packets (Zorb-

It, Inc.). In many cases, the low vegetation in front of the trap was cleared to increase the range of the sensor and visibility of animals to the camera. Whenever possible existing animal trails were utilized to set the cameras. Since all cameras were attached to trees, we limited our sampling to forest areas.

Cameras were placed approximately 50cm above the forest floor by strapping them to a tree with webbing straps and securing them with a bike lock, and were set to be active for 24 hours a day for a minimum of 30 days but not exceeding 60 days (to account for bad weather and other factors limiting retrieval). The delay (time between pictures) was set on 1 minute as a standard time for comparison purposes along the entire study. On some occasions cameras were set as pairs in order to acquire images of both sides of the animal, and such a capture event was considered as only one discrete observation for this study. All cameras collected data on date and time directly on the image, and all the cameras were synchronized with the exact time for every sampling period.

The rugged and broken terrain in the Talamanca Mountains presented a number of challenges for camera-trapping. During the study period, 198 camera-trap locations placed across a broad range of elevations (0-3600m) and management types (private and protected areas) were sampled. Cameras were aggregated in 16 sites, defined as groups of cameras sharing a similar elevation, stewardship and time period (Fig. 2). Within each site, camera-trap locations were systematically spaced 0.8 to 1.5 km apart. The need for variation in distance among camera placements was due to the broken terrain among study sites, as topographic barriers and other features prevented equal spacing in this mountainous environment. This nested hierarchical approach, where aggregations of camera-trap locations form sites, allows for a variety of analyses to be performed independently within the same study site.

A variety of information was calculated using these camera trapping techniques, including species richness, diversity and relative abundance. Species richness (*S*) is the measure of the absolute number of species captured or estimated in a given area. The relative abundance of species can also be measured in camera trap studies by calculating trap success (*TS*, sometimes referred to as capture success) (Kelly and Holub 2008), which takes into account both captures and effort and is useful to compare both among sites and among species. Species diversity is an index that assimilates both species richness and relative abundance information and can be measured using Simpson's index of diversity (*D*) (calculated using PCORD software, MjM Software). All three of these indicators can be calculated per trap location or summarized across different landscape variables, making them very useful indicators to compare mammal communities across elevation and stewardship categories.

Camera-trap locations and sites were selected with the goal of having a stratified random sample design, with an equal number of sample locations in lowland (<600m) and montane forests (>600m) and protected and private lands. The elevational cut off between lowlands and highland was based ecologically and opportunistically. Ecologically there is a gradual transition from flat swampy coastal communities to montane oak forests between sea-level and 1200m, and opportunistically, 600m allowed us to readily divide accessible areas into sampling categories. This division was only relevant on the Caribbean slopes since the Pacific slopes have been deforested below 1000m. Protected areas were defined as any property under the direct or indirect care of the Costa Rican government, including National Parks, Biological Refuges, Wildlife Refuges, and Indigenous Territories. Private lands were defined as any property owned by the private sector and included farms and private wildlife refuges.

In order to calculate the adequacy of the sample size, we used a variation of the species-area curve (using PC-ORD software) using a Chi-Squared distance measure, where "area" is the average distance between subsamples. In addition, we used both a first order (Heltshe and Forrester 1983, Palmer 1990) and a second order jackknife estimator (Burnham and Overton 1979, Palmer 1991) of species diversity, which are nonparametric re-sampling procedures that estimate the probability that a species was present and not captured during the sample. For our purposes, we are interested in knowing if our sample size is adequate to confirm the absence of several species presumed to have been extirpated from the study site.

We used one-way ANOVA (Minitab vers.15) with a 95% confidence level to determine significant relationships among study site categories and measured camera trap response variables (trap success, species richness, Simpson's diversity index). ANOVA results are also summarized to make observations about aggregations of camera trap locations (ie sites). Trap success was calculated as captures/trap nights x 100 (captures per 100 trap nights), and species richness was calculated by summing the number of species found at each site or location.

Results

During the 4 year study period we surveyed 16 sites, containing 198 camera-trap locations. A total of 21 cameras either malfunctioned or were stolen, and were, therefore, removed from the analysis. Thus, we analyzed data from 177 camera trap locations total; 49 in lowland private property, 62 in lowland protected areas, 46 in montane private properties, and 20 in montane protected areas. The discrepancy in sample size among sites reflects lost and stolen cameras as well as difficulty in accessing 1) high elevation protected area sites and 2) lowland private property. To compensate for this discrepancy, we used trap success as a surrogate for relative abundance, as it takes into account uneven sampling designs by calibrating results using the number of trap nights per sample.

We sampled for a total of 8,133 trap nights (24-hour periods) and obtained 2,446 photographic events that contained wild mammals (dogs and humans were not counted). We use a species-area curve to evaluate the sample adequacy; this method also measures the rate of "diminishing returns" in capturing new species by the addition of more camera locations (effort). The results of this analysis indicate that with only 50 camera locations (subplots) we were able to capture approximately 25 of the 30 species found (83%). Thus, the addition of over 100 more locations only had a return on effort invested of an additional 5 species (17%). However, due to the rarity or some species, the possible extirpation of others, and the numerous extrinsic factors in the study site which could influence trap success, we intentionally over-sampled.

The overall trap success for mammals captured was 30.1 per 100 trap nights. A total of 35 species were photographed during this study including 30 mammals (Table 1), 4 birds (*Armides cajanea, Crax rubra, Leptotila cassinii,* and *Tinamus* sp.), and 1 reptile (*Iguana iguana*). The estimate of total number of mammalian species found in the study area ranges from 34 (First-order jackknife estimate) to 36 (Second-order jackknife estimate), suggesting that although the sample size was more than adequate, we could have missed as many as 4 to 6 species.

Mammals were captured from nine taxonomic Orders and twenty Families. Among the Orders, the greatest diversity of species was found in Carnivora (n=13), followed by Rodentia (n=6), Didelphimorphia (n=3), Cetartiodactyla (n=2), Primates (n=2), Pilosa (n=1), Cingulata (n=1), Lagomorpha (n=1), and Perissodactyla (n=1). Within the most diverse Order (Carnivora) we recorded 6 species of cats (Felidae), 6 species of small carnivores (3 Procyonidae, 2 Mustelidae, and 1 Mephitidae), and one invasive Canidae (Coyote).

The most abundant Orders in term of number of photographs taken were Rodentia (n=926), followed by Carnivora (n=702) and Didelphimorphia (n=386) and the corresponding Families with the highest capture rates were Dasyproctidae, Didelphidae and Procyonidae. These figures are driven almost entirely by the three species with the greatest trap success (*TS*): Central American Agouti (*Dasyprocta punctata)* (*TS*=9.63), Black-Eared Opossum (*Didelphis marsupialis)* (*TS*=4.51), and White-Nosed Coati (*Nasua narica)* (*TS*=3.05) (Fig. 3). Although these common species are important prey items for the larger carnivores, it is notable that none of them are specifically targeted by hunters. Impacts of hunting on species diversity and distribution are discussed in Chapter 3 (this dissertation) and, thus, will not be addressed in detail here.

The carnivore community is particularly diverse, representing nearly half (43%) of the species captured and occurring from sea-level to at least 3600m. The most abundant carnivores, based on trap success are the White-Nosed Coati (TS=3.05) and the Northern

Raccoon (*TS*=1.22). Only one Canid, the Coyote, is confirmed from this site, and it is a recent invasive species (Hidalgo-Mihart et al. 2004) and found predominantly at higher elevations. Among the six Felid species present, none are common, but many are widespread. The Margay and Ocelot both occur in 69% of the sites sampled, but they are never abundant (*TS*=0.43 and 0.68, respectively). The Little Spotted Cat was only found at the high elevation in this study (González-Maya and Schipper 2008) and is know from only two photographs at the same location (likely the same individual). The Jaguar and Puma, although previously known from across the study area, are now rare and patchily distributed with high abundances in some areas, but mostly absent or less abundant in the majority of the region (González-Maya et al. 2008). The Greater Grison was the least trapped species (n=1) during the study.

Species richness, or the number of species per sampling unit, varied from 1-8 species among camera-trap locations and from 3 to 21 species among sites. Interestingly, we found no significant difference in species richness (ANOVA, F=1.03, p=0.31, n=177) or species diversity (ANOVA, F=2.17, p=0.142, n=177) between montane (n= 66) and lowland (n=111) sites in the study area. However, trap success was significantly higher in lowland than in montane sites (ANOVA, F=4.73, p=0.031). Although this finding is contrary to what we expected based on mammal species as whole, it does reflect species turnover (Beta-Diversity) between lowlands and highlands among medium and large mammals. For example, the Northern Tamandua, was only found below 1000m elevation in the Caribbean lowlands and foothills (the now extirpated Giant Anteater, a close relative, was also historically only found below 600m). In addition, two species (Dice's Cottontail and Baird's Tapir) were only found well above 600m elevation.

Among sites, the greatest species richness was present at Finca Las Alturas (n=21) followed by Hitoy- Cerere Biological Reserve (n=17), while Valle del Silencio (n=3) in La Amistad National Park and La Marta Wildlife Refuge (n=4) had the lowest richness (Table 2). Species relative abundance among sites follows a different pattern. The highest trap success was found in Yorkin, followed by Hitoy-Cerere, Finca las Alturas and Cahuita National Park (Fig. 4).

Both species richness (ANOVA, F=8.75, p=0.004) and species diversity (ANOVA, F=9.48, p=0.002) are significantly different in private (n=95) vs. protected areas (n=82), with no significant difference in trap success (ANOVA, F=0.32, p=0.569). There are significant differences in richness (ANOVA, F=29.33, p=0.000), diversity (ANOVA, F=25.65, p=0.000), and trap success (ANOVA, F=6.81, p=0.011) between private (n= 46) and protected (n=20) sites in montane areas, but no significant difference between richness (ANOVA, F=0.74, p=0.390), diversity (ANOVA, F=1.15, p=0.287), or trap success (ANOVA, F=2.94, p=0.089) in private (n=49) and protected (n=62) sites in lowland areas (Fig. 5 a,b,c).

Trap success (ANOVA, F=2.81, p=0.018), species diversity (ANOVA, F=3.39, p=0.006), and species richness (ANOVA, F=3.55, p=0.004) were all significantly different among stewardship categories (biological refuge n=23, indigenous territory n=25, national park n=30, private land n=26, private land under conservation n=69, and wildlife refuge n=4), with trap success highest in biological refuges and the lowest in wildlife refuges (Fig. 6 a,b,c).

Discussion

Our results indicate three patterns relative to the diversity and abundance of mammals within the study area. First, there is no significant difference between diversity and abundance inside and outside of protected areas in lowland forests. Second, private property retains significantly higher diversity and abundance in montane forests then in lowland forests. Last, private conservation lands have higher richness, diversity and abundance than the national parks that are designed and maintained specifically for species conservation. In fact, only biological refuges performed better than private conservation areas and only for trap success. These patterns are surprising and suggest that the designation of protected area status alone is not sufficient to conserve medium and large mammals in Costa Rica, and that without enforcement of existing hunting laws both private and protected areas are negatively impacted by illegal hunting.

Based on previous studies, we would expect that mammal diversity would decrease dramatically with elevation, yet in this study it did not. Palminteri et al. (1999) modeled elevational patterns of mammal diversity in the Talamanca mountains in the absence of deforestation, using known distributional limits. Their results indicate that, at least in theory, mammalian richness decreases with elevation along both slopes of the cordillera. However, in reality the majority of the natural vegetation has been lost on the Pacific (especially below 1,500 m) and increasingly on the Caribbean (Sánchez-Azofeifa et al. 2002), thus the impacts of land use change and hunting have likely greatly altered these patterns. There are two possible reasons why we do not see a decrease in diversity of medium and large mammals with incrased elevation in the study area; 1) much of the lowland forests have been lost and what remains is severely fragmented, and 2) there is sufficient species turnover between lowlands and highlands to ultimately balance the richness values.

In the lowland portion of the study area, the lack of any significant difference between diversity or abundance inside or outside of protected areas is startling – but very revealing of patterns across much of the lowlands of Central America. In our study area, there are no large stands on continuous forests below 600m, unlike the montane portions. The lowland alluvial plains are very productive for agriculture and have long been converted to human land-use (Dahlquist et al. 2007), and hunting is common (Chapter 3, this thesis). Remaining forests are in small protected areas and private farms, but in general there is little enforcement of hunting law. The exception is Cahuita National Park, which is very small and very well protected (over 20 park unarmed guards). However the case of Hitoy-Cerere is more typical; a large area with almost no protection afforded (only 2 park guards).

In the montane portion of the study area, the significantly higher diversity and abundance on private lands is also revealing, but for a very different reason. Most of the remaining forest cover on the Pacific slopes below 1500m is on private land, the largest of which is managed as a private wildlife refuge. This property, Finca las Alturas, has at least 16 armed guards who patrol 10,000 hectares. Because the majority of our sample in montane areas was above 1000m and the only non-protected forests are in this private farm, our data reflect the impact of hunter exclusion. Finca las Alturas has very high diversity and abundance of mammals compared to the nearby national park, and although we do not have data clearly showing this relationship, we can infer that it is because of the enforcement of national hunting laws. In this same area, La Amistad National Park has few if any guards. In fact, during this study several guards who attempted to pursue hunters were threatened and forced to abandon their posts.

Thirty mammal species were captured during this study, which is comparable to other similar mammal surveys using these techniques (Silveira et al. 2003, Trolle and Kery 2005), even though our trap effort far exceeds comparable surveys (Carrillo 2000, Tobler et al. 2008). At the broadest scale, we did not observe a notable reduction in species diversity with increasing elevation, as expected based on global mammal trends, signifying that medium and large mammals do not follow the diversity trends of mammals generally. As mentioned above we see a species turn-over (beta diversity) moving from lowland to montane forests, with Northern Tamandua confined to lowlands, and in this case, Little Spotted Cat, Baird's Tapir, Dice's Rabbit, Salvin's Spiny Pocket mouse and the Coyote confined to montane regions. Baird's Tapir, typically a lowland species (González-Maya et al. 2009), was only observed in the lowlands from two corpses killed by hunters in the Cerere River (in Hitoy-Cerere Biological Refuge). This observation is a fairly clear indication that lowland habitat loss and hunting are a serious concern for this species.

An additional consideration at high elevation is the still unknown effect of the recent invasion of Coyotes in the Talamancas (Hidalgo-Mihart et al. 2004). Although only recorded from three photographs during this study, its abundance in the high elevation grasslands is apparent due to the quantity of scat present. The fact that only eight photographs of Dice's Cottontail were obtained seems suspiciously low, although we have no baseline for comparison. Dice's Cottontail is endemic to the Talamancas, and its range overlaps entirely with the Coyote, which is cause for some concern.

Although our sample adequacy was very high, we still failed to capture at least two large terrestrial mammals that we expected to find and were once common in this region, Giant Anteater (*Myrmecophaga tridactyla*, previously confined to lowlands) and White-lipped Peccary (*Tayassu pecari*). Another species not recorded in any camera-trap was the White-Tailed Deer (*Odocoileus virginianus*), but we did find several tracks in areas we did not survey (and have seen it as a pet in the indigenous territories). Although our results suggest these species are absent, they are not conclusive as these species could occur in such low densities that they were not captured or they are no longer present in the sites sampled within the study area. In either case, the absence of these species from our study is cause for concern regarding their conservation status.

Several other species in the study are exceedingly rare and may also merit concern. The Little Spotted Cat was only recorded from the top of the Chirripó Massif (3,600m) in páramo forest enclaves, and although the species is known to frequent higher elevations in the Talamancas (Gardner 1971, González-Maya and Schipper 2008), it is found to sea-level in South America (de Oliviera et al. 2008). The paucity of information on this species generally and the lack of any records below 1000m in Central America suggest that this subspecies may be distinct from its disjunct South American relatives. The fact that we spent thousands of trap nights in appropriate habitat and only recorded one individual (in two photos) suggests that the species is very rare and we do not fully understand even its basic natural history. It may be worth noting that the area where we recorded the Little Spotted Cat does not have Ocelot, thus the possibility that smaller spotted cat populations are suppressed by Ocelots cannot be discounted (Tadeu de Oliveira, pers. comm.). We only obtained 4 records of Jaguarondi, a common small cat, which is frequently seen along trails, near roads, and in pastures. This species is seldom recorded in forested areas, and thus its absence from forest surveys is not as surprising.

A confounding factor for any camera-trap study is detection probability, which varies among sites and species. By adopting a standardized methodology (protocol) for trap placement, investigators can minimize the bias associated with where a trap is placed (on/off game trails), lures usage, trap height, and other factors. However, the ecology of target species also influences their probability of capture, most notably for small and/or arboreal species. Arboreal animals have less chance of being captured in terrestrial camera-traps, as the cameras are located on the ground. Small rodents have a small heat signal, so their probability of capture differs from location to location based on the ability of the heat-in-motion sensor to detect small heat signals. Three rodents are likely underestimated by this sampling technique (*Proechimys semispinosus, Heteromys desmarestianus* and *Liomys salvini*), while the Red Tailed Squirrel (*Sciurus granatensis*), although frequently captured (n=48), is both small and arboreal and, thus, is also undercounted. Arboreal, medium sized mammals are also underestimated, including the Mantled Howler Monkey (*Alouatta palliata*) White-Throated Capuccin (*Cebus capucinus*), Black-Eared Opossum (*Didelphis marsupialis*), and Kinkajou (*Potos flavus*). In fact, some noctural arboreal species such as Kinkajou will avoid an area where there are camera-traps after they have been photographed, presumably due to an aversion to the bright flash (Schipper 2007). In addition, semi-arboreal species are likely only captured during the portion of their lives spent on the ground, so their abundance is also underestimated, albeit to a lesser degree. These species include Northern Tamandua (*Tamandua mexicanus*), Margay (*Leopardus wiedii*), Tayra (*Eira barbara*), and White-Nosed Coati (*Nasua narica*).

How effective are protected areas at conserving medium and large mammals?

Within the region, protected areas play a vital role in preventing deforestation, but are less able to prevent hunting as few protected areas have the capacity or resources to enforce hunting regulations. Each protected area type also has different management protocols. Of the protected area types occurring in the study area, the highest legal protection is given to biological reserves, which are predominantly used for research and conservation purposes with little emphasis on tourism or other uses. National parks follow as the second most stringent level of legal enforcement, but they have much higher visitation rates because tourism is also a focus. Wildlife refuges are multi-use areas and have the least stringent conservation laws. Although indigenous territories are often cited as protected areas, they are, in fact, autonomous government-held properties managed by the local indigenous authorities where hunting still continues. In Costa Rica, private conservation areas (also called private wildlife refuges) are increasingly being recognized for their ability to protect biodiversity, albeit often on a relatively small scale (Langholz et al. 2000).

Our results indicate that in the Talamancas, biological reserves have greater trap success than other land management types. This figure is driven entirely by the Hitoy-Cerere Biological Reserve, the only one of its kind in the study area, and suggests that there are still many mammals present at this site. However, this figure fails to highlight that over half of all captures (63%) were of a single species, the Central American agouti and that we failed to capture Baird's Tapir or Jaguar, which we would expect to find in this habitat. This reserve is surrounded on 3 sides by indigenous territories (BriBri, Cabécar and Tayni) and had some of the highest levels of visible hunting signs, including hunting platforms and extensive networks of hunting trails; additionally, during our study we found the carcass of two Baird's Tapir in the river that had been shot somewhere upstream.

Private conservation areas showed the next highest trap success, and these figures are also driven by a single site, Finca las Alturas. Although this site is at mid elevation, it retains the largest populations of many lowland species, including Jaguar. This site is exceptional because it is the only area containing all of the expected mammal fauna for its elevation and often in abundance.

Indigenous territories had the third highest trap success rates. The majority of our effort was in the Keköldi Indigenous Territory which, despite being surrounded by banana plantations, highways and large towns, retains a rich mammal fauna. Although local authorities patrol the area, illegal hunting from migrant banana plantation laborers and surrounding non-indigenous peoples does take a toll on the few remaining larger mammals. This site hosts abundant small spotted cats and many medium sized mammals, but no Jaguar, Puma, Baird's Tapir, or Red Brocket Deer.

The relatively low trap success of national parks is driven primarily by Cahuita National Park, which is primarily focused on marine (coral reef) protection. The terrestrial portion is bound on one side by the coastline and on the other by agricultural activities and a highway. Although it is over 16km long, it is only approximately 2km wide on land and, thus, not ideal for conserving large fauna. However, this site is the only area where we photographed two primates, Mantled Howler Monkeys and White-Faced Capuchins, both of which come to the ground to cross open areas in the coastal swamp forests.

Private non-conservation lands are those maintained by private land owners often within a working farm with no focus on biodiversity conservation. It is not surprising that that trap success was low in these sites as they are often small to medium sized patches of disjunct forest and frequently excessively hunted (usually illegally by people other than the owners themselves). More surprising is the fact that wildlife refuges had the lowest trap success along with the highest theft rate of camera-traps. The primary reason our sample size is so low in this management type is that most of our data was lost due to theft in the Gandoca-Manzanillo Wildlife Refuge. These two pieces of information and the fact that the species we did capture were fairly common, human-tolerant species, suggest that hunting is widespread. However, further research by alternative methods is needed to confirm this finding.

Conclusions

Our study indicates that even the expansive system of protected areas in the Talamanca region is not enough to prevent the loss of native species. Although protected areas are an extremely valuable for conserving forests (ie habitat), there are seldom sufficient resources available to protect against illegal hunting. Deforestation and habitat fragmentation are having a clear impact on species distributions and diversity in these areas, and many lowland species are being marginalized into montane habitats, as that is all the forest remains in many areas. While rates of forest loss have declined and have even reversed in some areas, mammal populations continue to decline, most likely due to illegal hunting – which needs further research. Hunting, although prohibited by law, is a social and cultural norm in the Talamancas (Gaudrain and Harvey 2003) and is often not addressed by resource managers due to its controversial nature.

Planning organizations, local governments, and communities often assume that the biodiversity of the Caribbean portion of the Talamancas is well protected because the region appears predominantly forested. However, our results indicate that the mammal fauna across much of the lowlands is heavily degraded, most likely due to illegal hunting and effects of fragmentation. Thus although the forest remains in many areas, they are becoming “empty forests” with very few of the original large mammals remaining. In some areas we have documented effects of an “empty forest” syndrome (Redford 1992) in which all of the large mammals have disappeared entirely and the remaining species are those that can adapt to human presence and are not hunted. This situation is found especially in sites far removed from the core conservation areas (Cahuita, San Miguel, Carbón Uno, Carbón Dos, ASECODE, and Bocuare), but is increasingly common even in the sites that form the buffer zone around the Biosphere Reserve (Hitoy-Cerere, La Marta and Yorkin). From these patterns we can infer that although the lowland forests have been historically cleared (Pacific) and fragmented (Caribbean), they are now losing much of the mammal fauna due to hunting and land-use change. As a result, lowland species that cannot tolerate hunting and human-dominated landscapes appear to be increasingly marginalized into the remaining montane forests or are being lost all together.

Our results also indicate the importance of private conservation initiatives, especially well managed private lands surrounding the existing protected area network. For example, Finca las Alturas is the only site we sampled which retains large populations of large predatory species, Jaguar and Puma, largely extirpated from almost every other site sampled. This presence is explained by the difference in resources available for site level conservation and enforcement efforts; the 10,000 ha Finca las Alturas has approximately the same number of “park guards” as the 200,000 ha La Amistad National Park. The other difference is that the guard stations within the park system have either been abandoned (Tres Colinas) or are so understaffed that personnel cannot leave the station to conduct routine patrols (Hitoy-Cerere). The result is that there is almost no enforcement of laws in the park system, and therefore illegal hunting appears to be occurring in all parks and refuges in the Talamanca Region. The few large private landholdings that actively work to conserve wildlife are some of the last refuges for wildlife.

The conservation status of mammals in the Talamanca Region of Costa Rica is poor relative to what we would expect based on the number of protected areas. Lowland protected areas have lost many of the large carnivore and herbivore species, and the recent invasion of the coyote in the highlands is impacting the endangered Dice's Rabbit (Smith and Boyer 2008) and native competitors such as Puma. There is insufficient enforcement in the protected area network to protect targeted species, as hunting prevention and enforcement requires active patrolling and a permanent presence in the areas being "protected". In the time it has taken to conduct this study, several park guard stations have been abandoned and staff are increasingly centralized in offices away from the areas being protected.

The protected area system has been more effective at controlling deforestation rates, although some illegal logging still occurs along park boundaries. However, in the Caribbean lowlands protected areas are dispersed, disjunct, and not representative of the biodiversity present (Powell et al. 2000). The Talamanca-Caribe Biological Corridor is taking active and important steps, together with many local stakeholders, to replant forest and restore this natural linkage (Chapter 3, this thesis). However, if illegal hunting is not controlled, then no amount of restoration and forest conservation will restore medium and large mammals. With no remaining lowland habitat on the Pacific flanks of the Talamancas, probably the only hope for conserving forest- dependent lowland mammals is on Osa Peninsula – far removed from the Talamanca Mountains

One factor stands out above the others as limiting possible data analysis, the inverse relationship between species diversity and anthropogenic factors along an elevational gradient. Expected elevational patterns are canceled out by anthropogenic patterns, making it very difficult to define the explanatory variables. In this case, this effect is compounded by the fact that the principle threat to many of the species occurring in lowlands is hunting. We have no way to quantifiably measure this threat across the study site as we do for other anthropogenic factors which we can measure from aerial photographs or satellite images. There is no measurable factor to explain human decisions on where and what to hunt – decisions vary among cultures, ages, social norms, and economies, and change annually, seasonally, and based on wants and needs.

In conclusion, we have presented herein the first assessment of the patterns of the diversity and abundance of medium and large mammals in the Talamanca and how they relate to some ecological and anthropogenic factors. Our research has resulted in far more questions than answers, which we have tried to document and highlight so that efforts can be directed at filling the large knowledge gaps of the mammals of the Talamancas. However our overarching observation is that designation of protected areas is not enough - that without enforcement of existing hunting laws even this huge protected area network cannot retain many mammals in the long term. The Talamancas are among the last refuges for many species in Central America (Jaguar, Baird’s Tapir, White-Lipped Peccary) and the only place in the world we can protect others (Dice’s Cottontail).

There is an additional need to define incentives for environmental services provided by private land owners who retain not only the forest, but also the fauna found therein. We have demonstrated a positive relationship between species richness and private conservation lands, especially those that also provide vigilance and enforcement of hunting laws. Currently, Costa Rica has a very strong ecosystem service payment plan in place for retaining forests on private property, and we propose an additional incentive for land owners to not only prevent illegal logging, but also illegal hunting.

This study seeks to inform national and local policy, through the results of an intensive wildlife survey, by demonstrating the strengths and weaknesses of protected areas in SE Costa Rica. Camera-trap techniques provide a unique tool for establishing base-line data and monitoring of medium and large mammal populations. Our findings could, therefore, be applied to similar efforts in the future to establish trends over time and to understand possible consequences of conservation policies on wildlife. We feel that a combination of private incentives and additional resources for parks and protected areas to combat illegal hunting, could eventually allow the recovery of many rare and extirpated species. We predict that, with no change in current policy and funding, the lowlands will become depauperate of medium and large mammals, and remaining lowland species will be pushed to the upper limits of their elevation tolerance. This research demonstrates the value of vigilance and enforcement of existing laws in protected and private tropical forest areas.

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Table 1. Mammal species, organized in taxonomic order, that were captured during the study (2005-2008). Mode=primary mode of locomotion (T=terrestrial, A=arboreal), Trap event=number of times captured, Total proportion=percent of trap events with that species.

Family	**Genus species**	**Common Name**	**Mode**	**IUCN Red List**	**Trap event**	**Total Proportion**	**Min. Elevation**	**Max. Elevation**	**Number locations**	**Percent locations**
Didelphidae	*Chironectes minimus*	Water opossum	T/A	LC	7	0.3%	204	1729	2	1.13
Didelphidae	*Didelphis marsupialis*	Black-eared Opossum	A	LC	367	15.0%	7	2330	63	35.59
Didelphidae	*Philander opossum*	Gray Four-eyed Opossum	A	LC	12	0.5%	13	1500	4	2.26
Myrmecophagidae	*Tamandua mexicana*	Northern Tamandua	T/A	LC	24	1.0%	7	589	15	8.47
Dasypodidae	*Dasypus novemcinctus*	Nine-banded Armadillo	T	LC	151	6.2%	7	2961	59	33.33
Atelidae	*Alouatta palliata*	Mantled Howler Monkey	A	LC	1	0.0%	13	13	1	0.56
Cebidae	*Cebus capucinus*	White-throated Capuchin	A	LC	4	0.2%	9	16	2	1.13
Cuniculidae	*Cuniculus paca*	Spotted paca	T	LC	65	2.7%	16	2167	27	15.25
Dasyproctidae	*Dasyprocta punctata*	Central American Agouti	T	LC	783	32.0%	7	2167	110	62.15
Echimyidae	*Proechimys semispinosus*	Tome's Spiny Rat	T	LC	14	0.6%	123	263	6	3.39
Heteromyidae	*Heteromys desmarestianus*	Demarest's Spiny Pocket Mouse	T	LC	15	0.6%	111	265	7	3.95
Heteromyidae	*Liomys salvini*	Salvin's Spiny Pocket Mouse	T	LC	1	0.0%	1450	1450	1	0.56
Sciuridae	*Sciurus granatensis*	Red-tailed Squirrel	A	LC	48	2.0%	12	3132	28	15.82
Leporidae	*Sylvilagus dicei*	Dice's Cottontail	T	DD	26	1.1%	1426	3599	8	4.52
Canidae	*Canis latrans*	Coyote	T	LC	7	0.3%	3394	3599	3	1.69
Felidae	*Leopardus pardalis*	Ocelot	T	LC	62	2.5%	15	2557	33	18.64
Felidae	*Leopardus tigrinus*	Little Spotted Cat	T	VU	2	0.0%	3599	3599	1	0.56
Felidae	*Leopardus wiedii*	Margay	T/A	NT	39	1.6%	13	1600	28	15.82
Felidae	*Panthera onca*	Jaguar	T	NT	47	1.9%	349	1950	18	10.17
Felidae	*Puma concolor*	Puma	T	LC	96	3.9%	264	3139	35	19.77
Felidae	*Puma yagouaroundi*	Jaguarundi	T	LC	4	0.2%	170	503	4	2.26
Mephitidae	*Conepatus semistriatus*	Striped Hog-nosed Skunk	T	LC	49	2.0%	7	1950	30	16.95
Mustelidae	*Eira barbara*	Tayra	T/A	LC	38	1.6%	14	1945	24	13.56
Mustelidae	*Galictis vittata*	Greater Grison	T	LC	1	0.0%	155	155	1	0.56
Procyonidae	*Nasua narica*	White-nosed Coati	T/A	LC	248	10.1%	7	3132	70	39.55
Procyonidae	*Potos flavus*	Kinkajou	A	LC	1	0.4%	8	1323	2	1.13
Procyonidae	*Procyon lotor*	Northern Raccoon	T	LC	99	4.0%	7	1269	27	15.25
Tapiridae	*Tapirus bairdii*	Baird's Tapir	T	EN	95	3.9%	1522	3599	17	9.60
Cervidae	*Mazama temama*	Central American Red Brocket	T	DD	11	0.4%	215	2167	10	5.65
Tayassuidae	*Pecari tajacu*	Collared Peccary	T	LC	120	4.9%	73	3599	35	19.77

Table 2. Site characteristics. Elevation measured in meters. S=species richness and D=Simpson's diversity index

	Camera stations	Captures	Trap nights	Stewardship	Min. Elev.	Average Elev.	Max. Elev.	S	D
ACODEFO	28	359	1569	Private	139	343	478	15	0.79
ASECODE	4	23	136	Private	94	137	183	7	0.81
Bocuare	6	61	303	Private	73	163	247	10	0.82
Cahuita	14	148	494	National Park	7	12	28	13	0.83
Carbón Uno	3	17	96	Private	71	220	294	6	0.75
Carbón Dos	6	93	357	Private	206	239	258	9	0.80
Cerro Chirripó	9	59	540	National Park	2480	3190	2599	10	0.79
Cerro Pittier	10	124	600	Private	1612	1779	2330	13	0.58
Finca Las Alturas	39	611	1890	Private	1174	1496	2167	21	0.84
Hitoy-Cerere	23	382	904	Biological Reserve	142	370	598	17	0.58
Keköldi	25	278	1057	Indigenous Territory	48	138	230	15	0.71
La Marta	5	13	160	Wildlife Refuge	857	878	940	4	0.49
San Miguel	3	32	168	Private	51	53	55	8	0.79
San Rafael de Bordon	9	83	356	Private	161	174	184	8	0.65
Valle del Silencio	9	80	540	National Park	2390	2503	2587	3	0.07
Yorkin	4	76	176	Indigenous Territory	171	191	212	12	0.78

Figure 1. The study area in Costa Rica showing the orientation of protected areas and Indigenous Territories (IT) and remaining forest cover (light grey). A=Chirripó National Park (NP), B=Hitoy-Cerere Biological Refuge, C=Cahuita NP, D=Gandoca-Manzanillo Wildlife Refuge; 1=Tayni IT, 2=Cabécar IT, 3=BriBri IT, 4=Keköldi IT.

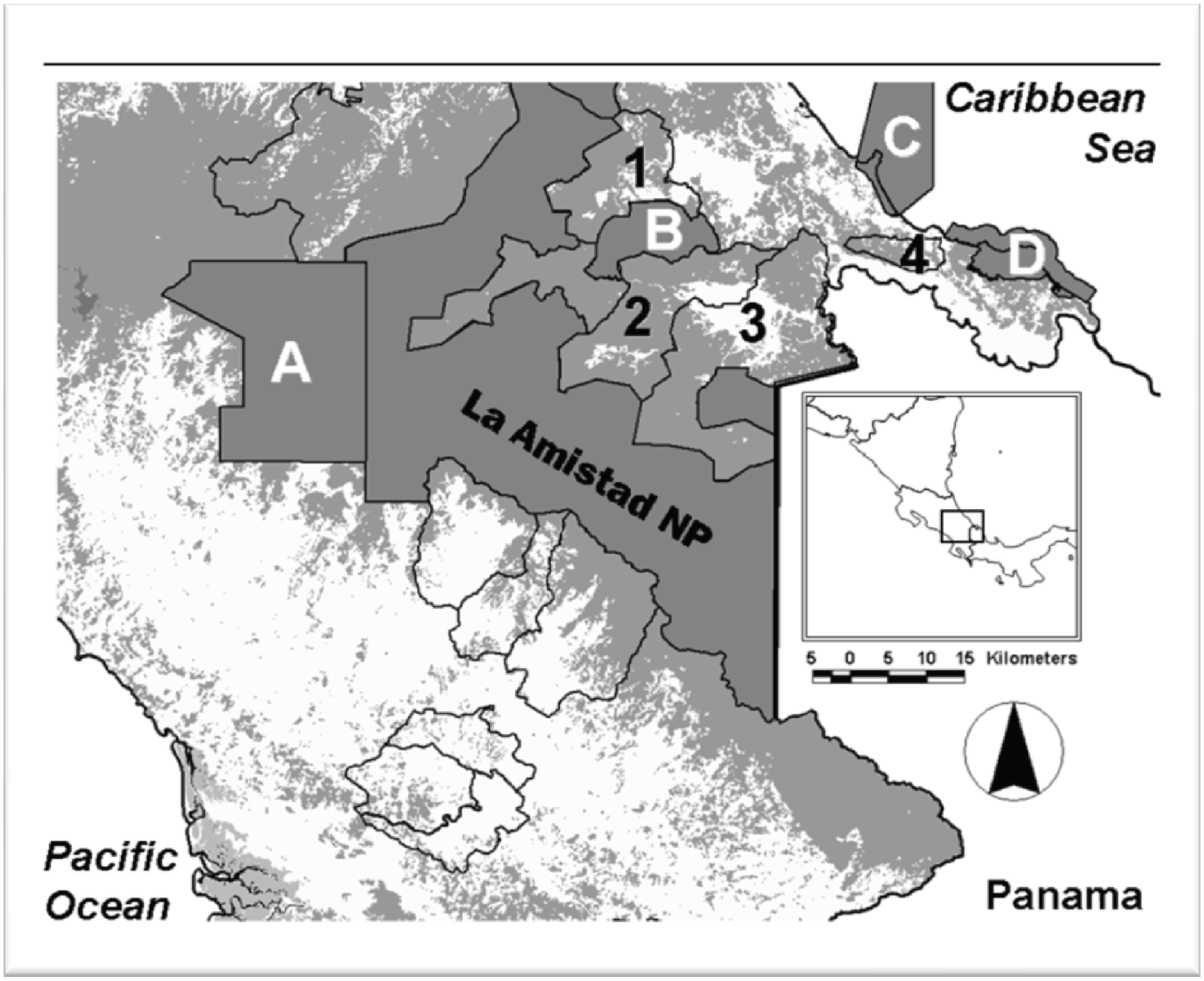

Figure 2. Sites depicted showing elevation (dark grey >600m, light grey <600m) and relief: 1=Finca las Alturas, 2=Cerro Pittier, 3=Valle del Silencio, 4=Cerro Chirripó, 5=La Marta, 6=Hitoy-Cerere, 7=Bocuare, 8=San Rafael Bordon, 9=ASECODE, 10=Cahuita, 11=Carbón Uno, 12=ACODEFO, 13=Carbón Dos, 14=Keköldi, 15=San Miguel and 16=Yorkin.

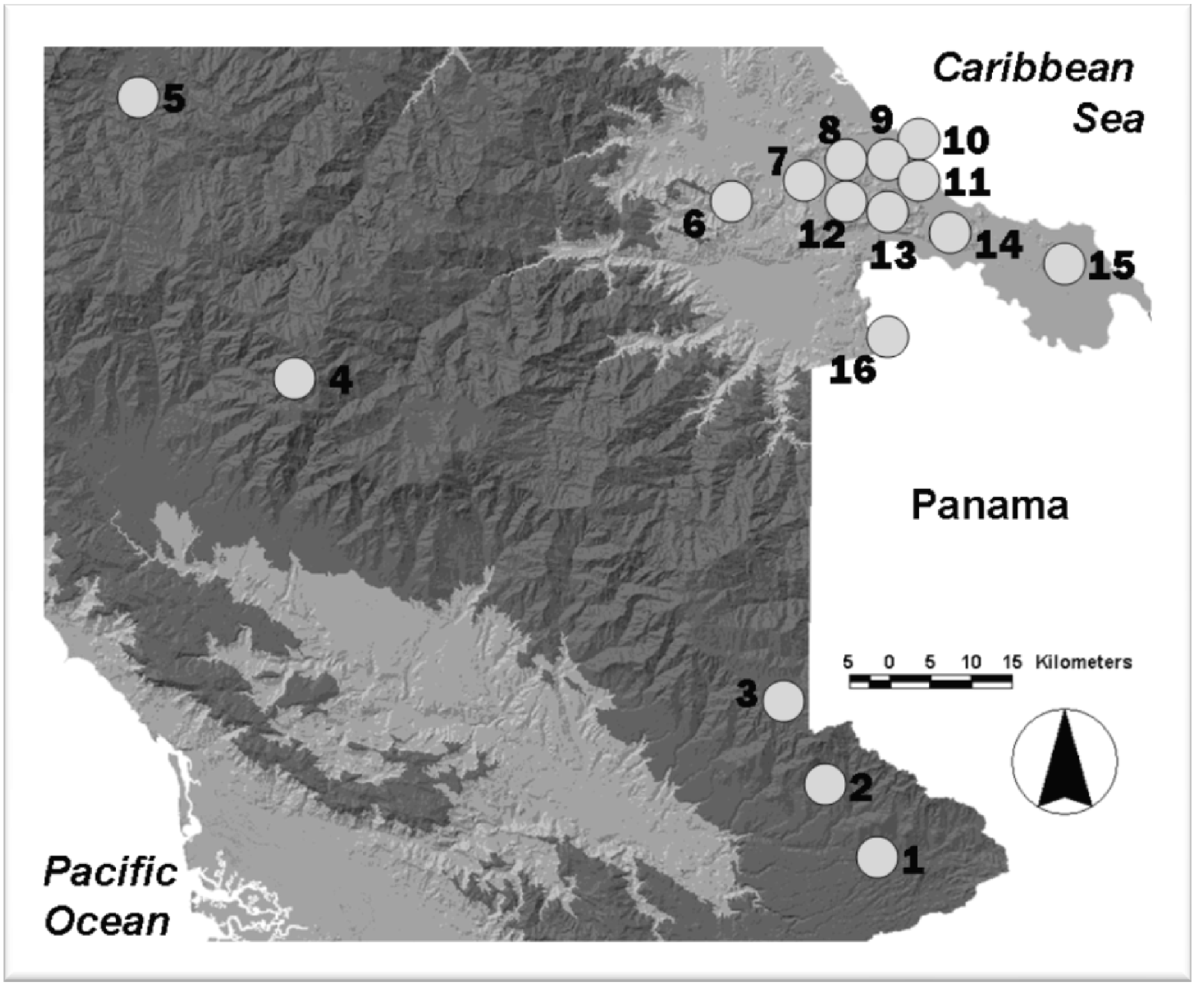

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Figure 3. Trap success (captures/trap nights x 100) and standard error for each species averaged across all camera trap locations.

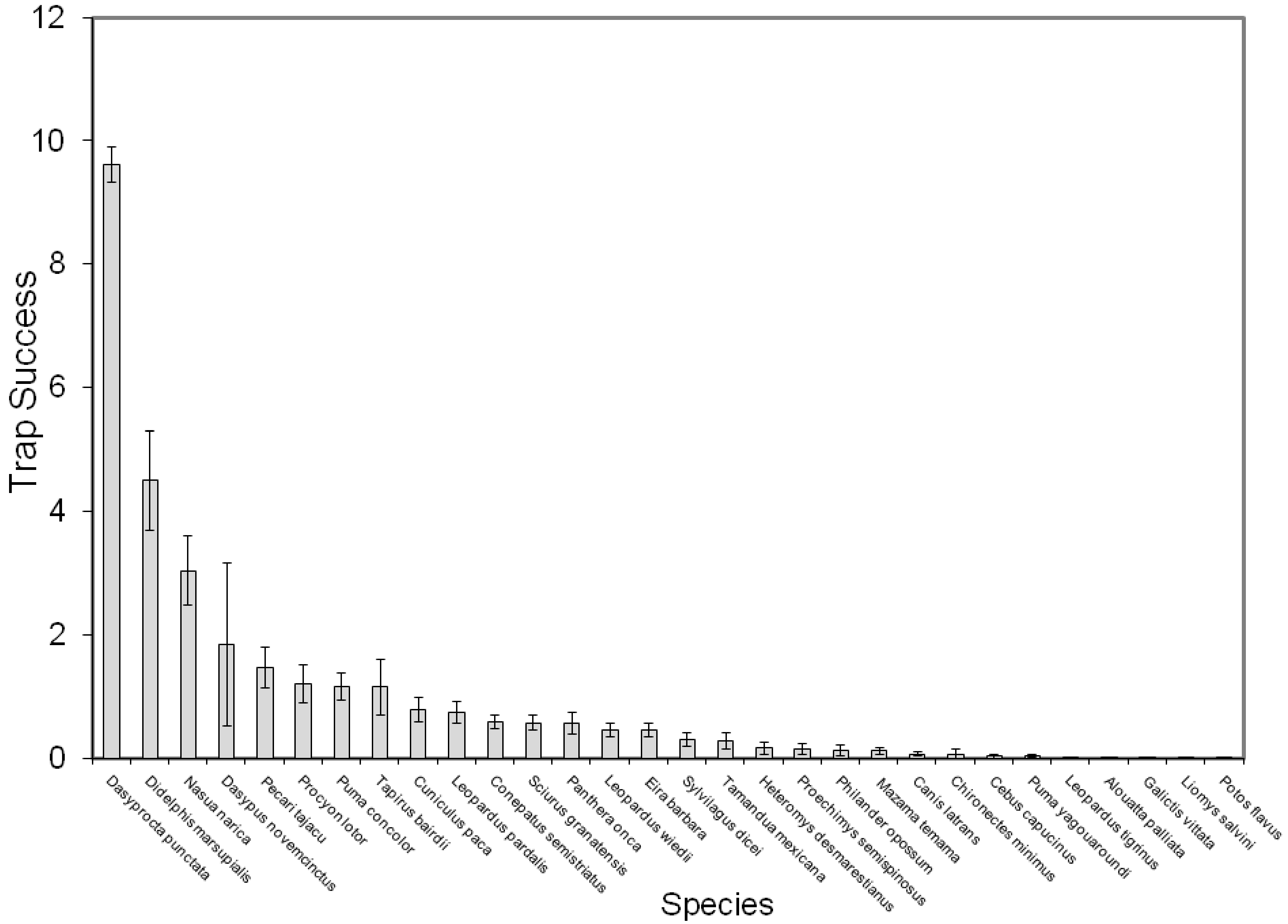


Figure 4. Trap success (captures/trap nights x 100) among sites.

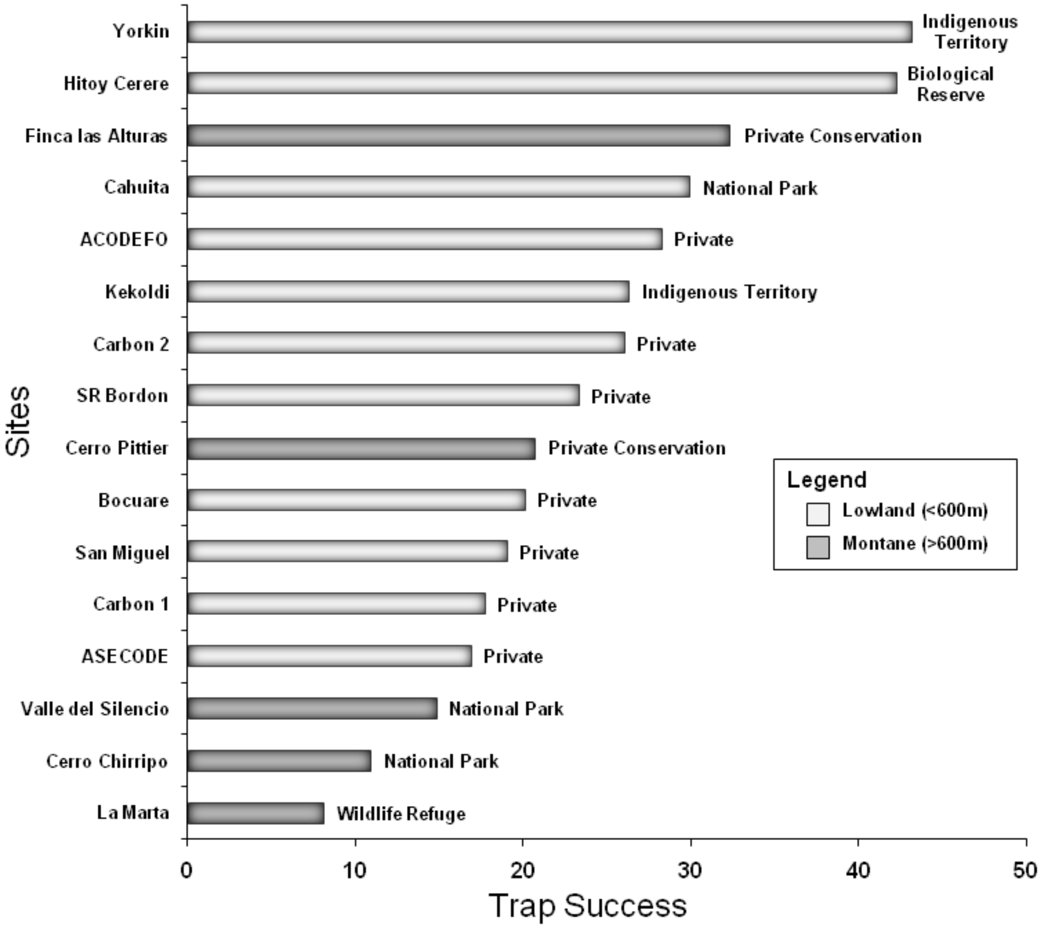


Figure 5. Box plots comparing diversity and abundance between private property and protected areas (reserves) within lowland (<600m) and montane (>600m) areas. Box width represents sample size, darker shading indicates private property and * indicates outlyer data points.

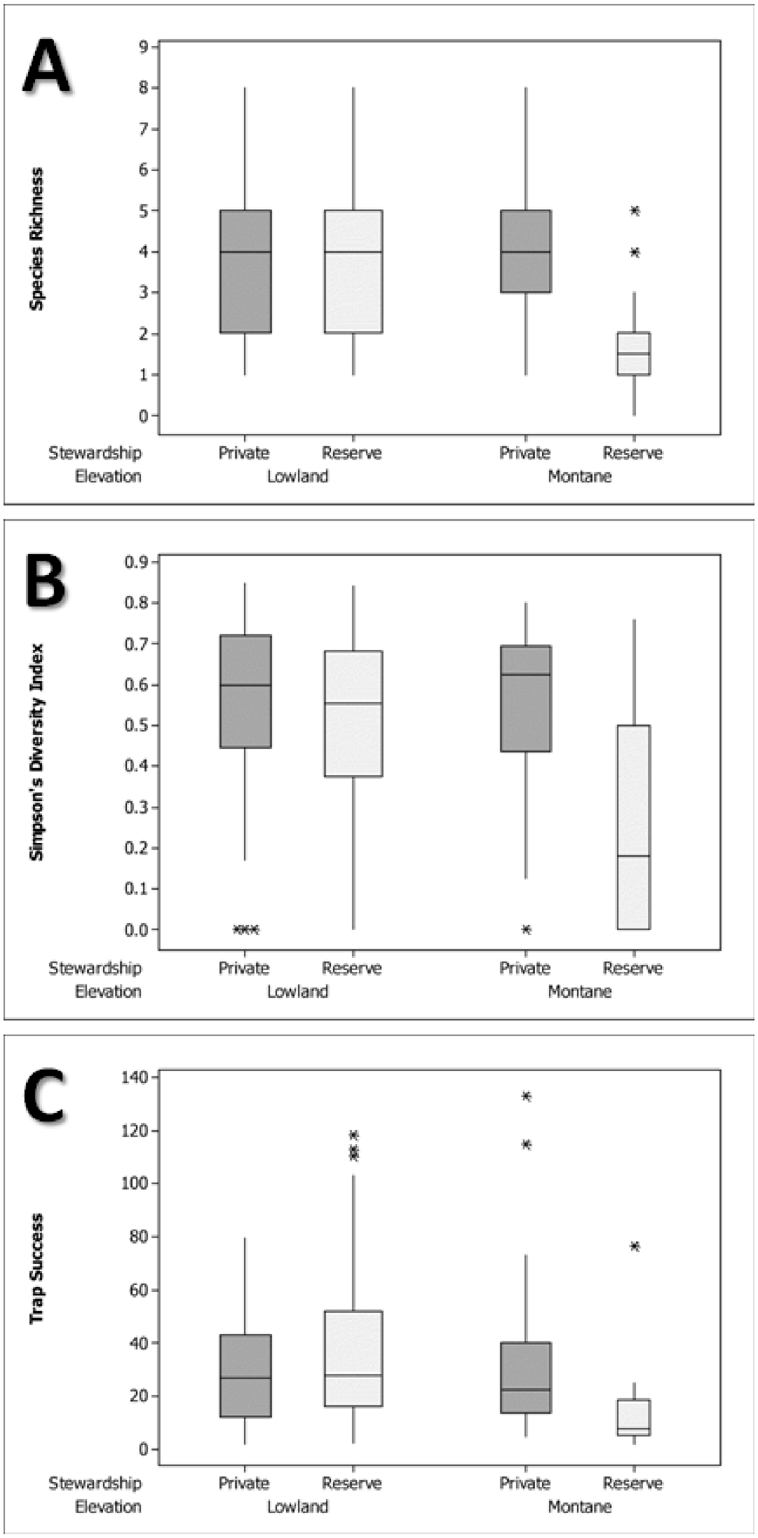
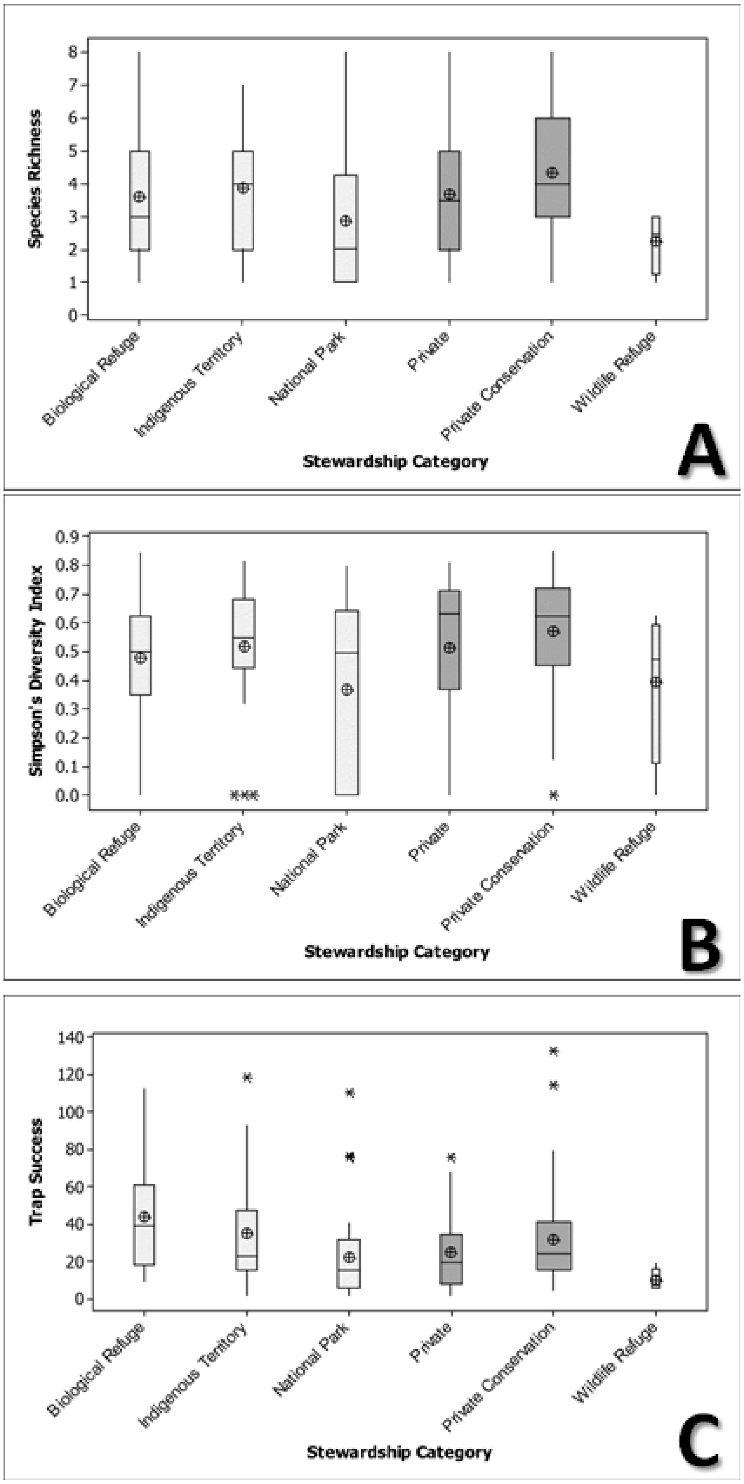


Figure 6. Box plots comparing diversity and abundance among stewardship categories. Box width represents sample size, darker shading indicates private property and * indicates outlyer data points.



Chapter Three

Human dimensions of wildlife conservation in the Talamaca-Caribe Biological Corridor, Costa Rica: mammal diversity, threats and local knowledge at the landscape scale

Abstract

Tropical forests in Central America have been reduced to a fraction of their natural extent, and the remaining forests are increasingly targeted by hunters. In order to better understand how wildlife populations respond to hunting, we surveyed human perceptions and wildlife diversity in the Talamanca-Caribe-Biological Corridor in the Caribbean lowlands of Costa Rica. We used data collected over 14 months of camera-trapping and local interviews to ask four overarching questions: 1) Are protected areas enough to conserve mammals in the corridor? 2) Is there a relationship between hunting and wildlife abundance and diversity? 3) What impact does wildlife conflict have on mammal populations? and 4) What impact does hunting have on mammal populations? Our results indicate that protected areas alone are not enough to conserve mammals, especially in a human-dominated landscape, and that the majority of mammal communities are highly modified due to hunting pressure. Sites with the highest species relative abundances, diversity and evenness were those least impacted by human disturbance and hunting. Hunting impacts species disproportionately across the region, and generally one or two species (especially Spotted Paca) are targeted. Human perceptions are generally positive towards protected areas and wildlife conservation, and local knowledge suggests that large mammals currently extirpated were once common in the region. Our study suggests that there are several opportunities for species and habitat restoration and that native wildlife would greatly benefit from 1) local and national enforcement of the existing hunting laws (especially in protected areas) and 2) the creation of environmental service payments and other incentives for land owners to retain wildlife on private property.

Introduction

Tropical forests around the world have been reduced to a fraction of their natural extent, and the combined impacts of habitat loss, fragmentation and hunting on native wildlife populations have pushed many species to the brink of extinction. Indeed, globally one-quarter of all mammals are threatened with extinction, and not surprisingly the driving threats are habitat loss and degradation (affecting 40% of mammals) and harvesting (affecting 17% of mammals) (Chapter 1, this thesis). Reserve systems have been put into place to reduce species loss; however, the effectiveness of reserves is more a function of actual land stewardship practices than of simply putting the land under formal protection. This situation is especially true in Costa Rica where nearly 20% of the country is protected and, although protected areas are important to halt habitat loss, the lack of connectivity and minimal enforcement of hunting prohibitions results in a reduction of wildlife populations (Chapter 2, this thesis). Herein we focus on four broad questions to allow us to explore relationships between wildlife populations and human actiuvities: 1) Are protected areas enough to conserve mammals in the corridor? 2) Is there a relationship between hunting and wildlife abundance and diversity? 3) What impact does wildlife conflict have on mammal populations? and 4) What impact does hunting have on mammal populations?

Conservation corridors have been proposed as a tool to increase connectivity among reserves by allowing species to move between protected areas and forest fragments (Bennett 2003, Hilty et al. 2006), yet their success has been debated (Beier and Noss 1998, Hobbs 1992, Simberloff 1992). However, by providing connectivity among protected areas, many corridors could encourage species movement across private lands, which potentially make them more susceptible to hunting and human conflict.

Costa Rica is well known for its protected area network, which currently includes approximately 12% of the national territory under some form of formal conservation. Additionally, 7% of the country is retained in various indigenous territories. Although expansive compared to many countries, the existing network of protected areas is neither representative of the available habitat nor well connected to allow for the movements and flows of species and ecological processes

(Powell et al. 2000). To remedy this situation, the Costa Rican government begun a systematic planning process to identify priority landscapes for biological corridor development (Garcia 1996). Among the priority sites identified to enhance connectivity of remaining habitats was the Talamanca-Caribe Biological Corridor in southeast Costa Rica (CBTC for its Spanish acronym), that proposes to connect a network of reserves from the continental divide to the Caribbean Sea across a human-dominated landscape. However, deforestation in the lowland "Atlantic Zone" in Costa Rica has been historically very high due to banana plantation and other agricultural expansion (Veldkamp et al. 2006). In this case, "human-dominated" refers to private properties that have been extensively converted to agriculture, pasture or agroforestry and have fragmented remaining native habitats.

Larger terrestrial mammals generally require large areas (i.e. landscapes) and are useful indicators of intact communities and ecosystems (Sanderson et al. 2002). Many of these "landscape species" are targeted by hunters (Robinson 1996, Carrillo et al. 2000), and in human-dominated areas, the combination of hunting and landscape conversion means that these species are often the first to decline or disappear. Therefore, their presence and abundance can act as an early indicator of ecosystem health. The challenge faced by conservation practitioners in human-dominated landscapes, such as the CBTC, is to work directly with local communities to mitigate the negative effects of the compounding threats of habitat loss and hunting.

Habitat loss and degradation have a wide range of impacts on wildlife. Some species benefit from habitat conversion, while others cannot tolerate even low levels of disturbance. In the Talamanca region, habitat loss is mainly due to loss of primary forest that has been converted to agriculture. In addition, logging plays a role in both partial and complete removal of forest cover (Frumhoff 1995). The direct results of forest loss are reduction in habitat connectivity across the landscape and fragmentation and reduction of habitat size (Fahrig 1997, Bennett 2003). Indirect results of forest loss include barriers to movement and dispersal of species (Bennett 2003), changes in physical processes (i.e. "edge effects") (Malcolm 1997, Kapos et al. 1997), increases in human access (Robinson 1996), and increases in landscape heterogeneity (Turner et al. 2001). Not surprisingly, Daily et al. (2003) found that with an agricultural matrix in western Costa Rica, species tolerant to landscape change were not relatively common, but rare, and threatened and non-tolerant species were absent from the landscape. The overall effects of habitat loss on a landscape are dependent on the spatial and temporal scales at which the changes occur and the tolerance of the individual species to these changes. Information is often lacking about both direct and indirect impacts of habitat loss on wildlife.

Although no comprehensive inventories of mammal fauna have been completed in the CBTC, the region may contain as many as 80 species of terrestrial mammals and as many as 200 mammal species in total, including bats and marine mammals (Wainwright 2002). The first survey of large mammals, using camera-traps, reported 30 species in the Talamanca region (Chapter 2, this thesis, González-Maya et al. 2007), while within the CBTC, Harvey et al. (2006) documented 27 mammal species using track counts and mist nets. At a broader scale, an estimate of the jaguar population in the Talamancas as a whole was lower than expected, with an estimated 340 mature individuals (Schipper et al. 2005). Thus, our current knowledge of the mammal fauna in the CBTC is severely limited and represents only a subset of the total number of species presumed to be present.

Studies conducted on the mammals used by the BriBri indigenous people in Talamanca have demonstrated the cultural importance of hunting (Gaudrain and Harvey 2002). In the Talamanca Region, there are several types of hunting that undoubtedly have distinct effects on the abundance and diversity of target species. In many indigenous territories people hunt for subsistence and are opportunistic in targeting prey (Gaudrain and Harvey 2002). In Panama, studies suggest that, in most cases, indigenous peoples do not go far from their villages and will take a wide variety of game (Smith 2008). Generally, indigenous hunters will take most medium and large mammals or birds they come across, depending on the season and location (Peres 2000). However, hunting for economic purposes will tend to target a single species (especially Spotted Paca in Costa Rica), while sport hunters often pursue large charismatic species. These different hunting types can lead to very different impacts on species community and population structure (Carrillo et al. 2003).

In rural agricultural communities, native species (especially predators) are sometimes perceived as a nuisance to livestock and pets and this can result in retaliatory killing and ill-feelings towards wildlife. Therefore, understanding the frequency of human-wildlife conflict is important in determining what measures can be taken to promote species conservation in landscapes dominated by humans (Treves and Karanth 2003, Michalski et al. 2006). In addition, this information is also useful in determining the condition of the surrounding mammal communities, as carnivores often target domestic animals as a result of the absence of native prey species (Conforti and Azevedo 2003) due to overhunting. In addition, understanding the perceptions of local residents towards wildlife and protected areas can be a fundamental step in addressing issues of conservation planning (Brandon 1996, Groves 2003, Schipper 2005). Interviews are an important means to collect information on local knowledge and on the historical distribution of species. Hunters can often share valuable information such as the last time they saw a species, where it was, and whether they know other people who have seen it. This information is especially useful for determining when species disappeared from a region and for validating whether the absence of records from a camera-trap is truly absence or simply non-detection. However, in some cases, conducting interviews with rural people about subjects such as illegal hunting can be a challenge, as it can be viewed as "self-incriminating". In such cases, it is necessary to frame interview questions in a non-invasive way or to ask indirect questions about sensitive subjects.

Healthy ecosystems provide many services to humans, including benefits to health and well-being. Humans rely heavily on functional ecosystems, especially in rural areas where the majority of residents depend on rivers and ground water for drinking, on soil retention and fertility for their crops and livestock, and on intact forests, rivers, and seas as sources of protein. In addition to conserving biodiversity, the conservation of forest resources has many benefits to local peoples, including protection of watersheds (water supply), controlling erosion, and public health (Myers 1997). Among the primary benefits local inhabitants obtain from the CBTC are the retention and improvement of the ecosystem services rendered from the surrounding landscape. The Costa Rican government has developed economic incentives for landowners who prevent logging and deforestation on their properties (Chomitz et al. 1999, Pagiola 2008). However, there is currently no economic incentive for landowners to retain wildlife within forests.

The potential ecosystem services provided by remaining intact forests and wetlands within CBTC are a strong selling point for biodiversity conservation in the region. Currently many local property owners are receiving Environmental Service Payments (ESP) for protecting forests on their properties. The role of CBTC in species conservation remains uncertain, however, especially for larger mammals and ground birds which are targeted for hunting and do not tolerate conversion of native forests to agriculture. The remaining habitat is fragmented and illegal hunting is common both in surrounding protected areas and on private properties (Chapter 2, this thesis). Redford (1986) coined the term “empty forests” to describe the phenomenon of forest ecosystems where vertebrates and other animals have disappeared due to uncontrolled hunting.

The CBTC, in connecting the montane La Amistad National Park to several coastal protected areas, spans a human-dominated agricultural landscape composed of private property and Indigenous Territories, which are the dominant land stewardship types within the corridor. The design of the CBTC allows us to ask some fundamental questions about the effectiveness of corridors at conserving wildlife between protected areas and what factors might limit wildlife in such human-dominated agricultural landscapes. For example, 1) what impact does hunting have on wildlife, 2) do residents within the corridor think wildlife is important, 3) are protected areas valued locally as a conservation tool, and 4) and how does wildlife respond to landscape conversion. Answers to these and many other questions provide important feedback to measure the success of the CBTC and to evaluate the effectiveness of conservation measures already in place.

The objectives of this study were to: 1) evaluate the human perceptions of wildlife and conservation within communities inside the CBTC, and 2) use these observations to evaluate the impact of hunting on native wildlife and suggest potential solutions. Because a cause and effect relationship between hunting and wildlife is difficult to disentangle from other co-occurring effects of habitat loss and degradation, we combined wildlife survey techniques with social survey techniques and evaluated the information spatially in a GIS system. Specifically, we took an interdisciplinary approach by combining wildlife surveys, local interviews and landscape analysis to evaluate aspects of species occupancy, hunting pressure, human perceptions of wildlife, and human-wildlife conflict within the CBTC.

Methods

Study area

The CBTC covers an area of 39,500 ha (395 km2) on land and 9,436 ha (94.3 km2) in the marine realm and extends from the near shore coral reefs to the boundary of La Amistad International Park in southeastern Costa Rica (from 09˚47'-09˚32'N, 82˚15'-082˚33'W). As currently delimited, the CBTC extends from the premontane foothills of the Talamanca Mountains (approximately 500m) to sea-level along the Caribbean coast, through a mosaic of protected areas, human dominated landscapes, and indigenous territories (Fig. 1). The private lands are composed primarily of banana plantations, agroforestry, cattle pasture, and patches of secondary and primary forest, while Indigenous Territories are a mosaic of small scale agriculture, agroforestry and native forest (Dahlquist et al. 2007)

The Holdridge life zones of the CBTC include both tropical humid forests and premontane wet forest life zones (Tosi 1969). At a finer scale, there are four types of predominant terrestrial vegetation: 1) flooded wetlands along the coastal plains which are dominated by grasslands; 2) swamp forest dominated by *Raphia taedigera* in flooded areas and *Pentaclethra macroloba*, *Xylopia frutescens*, and *Dipterix panamensis* in seasonally flooded areas; 3) flooded and semi flooded forest along rivers and streams dominated by *Prioria copaifera* and interspersed with *Pterocarpus* sp. and *Carapa guianensis*; and, 4) piedmont forests with emergent *D. panamensis and Lecythis ampla* and also characterized by *Tabeuia chrysanta, Hura crepitans*, and species in the families Lauraceae and Sapotaceae (Powell et al. 2001). Although there is some variation in habitats across the region, we would not expect significant variation in mammalian species composition among sites in the absence of human disturbance and hunting.

The principal population centers in the region are Bribri, Puerto Viejo, Cahuita, Sixaola, Shiroles, and Suretka, all together containing approximately 25,000 residents. However, these towns are not included in the biological corridor, which is focused primarily in rural areas (which have only 5,000 residents). Culturally, the region is a mix of Afro-Caribbean along the coast and Indigenous peoples (BriBri and Cabécar) along the western and central portions and in the foothills a mix of both these groups together with immigrants from Panama, Colombia, Nicaragua, and the rest of Costa Rica. This study focused on the rural communities and the wildlife remaining in forested areas.

Methods

This study brings human-interview data to bear on information collected in a region-wide wildlife survey (Chapter 2, this thesis). Integrating these datasets allows for comparison of local peoples' responses to interview questions with estimated species diversity and abundance among sites. We conducted 99 interviews with local residents who live in rural areas of the CBTC in order to better understand how often people hunt, which species they hunt, whether they are aware of any changes in mammal populations over time, and whether they are aware of the impacts of hunting on mammal populations. We targeted communities situated in and around forest-dominated areas, since our camera trap sites were confined to remaining forests. When possible, interviews were conducted in the near vicinity of the camera-trap locations, aiming to target residents close to these survey points (Fig. 2). Together, interview sites and wildlife survey sites were aggregated into locales, representing local communities from which we could make inferences (Fig. 3). Interview questions were designed to allow us to better understand relationships among species occurrence, hunting, human-wildlife conflicts, and human perceptions of both wildlife and conservation measures.

Local Knowledge

Interviews were conducted from October 2004 to December 2005 in 18 villages and towns, representing 5 communities: 1) Bribri/Buena Vista (BBV) (37 interviews), b) Bocuare/San Rafael/Carbón (BSC), (32 interviews), c) Coroma (COR) (11 interviews), d) Gandoca (GAN) (13 interviews), and e) Keköldi (KEK) (6 interviews) (Figure 3). Communities were defined based both on proximity and aggregated based on land use and culture. Coroma and Keköldi were indigenous communities nested within the BriBri and Keköldi indigenous territories, respectively. Both of these communities are governed by indigenous territorial governments;

individuals do not own their own land as it is community managed. Bribri/Buena Vista occurs on the border of the BriBri Indigenous Reserve and is a cultural mix of indigenous and non-indigenous people. Many of the residents work on local banana plantations and/or own their own farms, and the urban center (Bribri) lies just outside the Bribri Indigenous Territory. Bocuare/San Rafael/Carbón is a network of small towns in a mosaic of forest remnants, pasture, and small farming operations. Residents are almost entirely non-indigenous and the land uses are cattle ranching, small-scale crop farming, and small plantations. Gandoca is a coastal community near the Panamanian border, and residents are non-indigenous. Land uses also include cattle ranching and small farms, however, the residents primarily subsist on income from tourism and banana plantations. Data from the 5 communities were evaluated against 8 sites sampled by camera trap techniques. Four interview sites overlapped directly with wildlife survey sites, and one site (Coroma) overlapped indirectly. Three sites where camera trap data were collected did not overlap since no interviews were possible either because of logistical problems or lack of inhabitants to interview such as in a National Park.

Interviews were conducted by trained local field assistants to minimize any bias associated with "outsiders" asking sensitive questions about hunting and wildlife use. Within each community, a known cooperative family or individual was used to start each interview series (who was also the community contact point for the CBTC), after which we employed a "snowball" sampling technique by asking interviewees who else we should interview who might also be able to answer the questions we posed, based on their knowledge of animals and hunting. We also stratified the samples across the two major land stewards, private landowners and indigenous residents.

A total of 25 questions, both open ended and categorical, were asked within 4 major thematic categories: 1) human-wildlife conflicts; 2) hunting; 3) perceptions of protected areas; and 4) species knowledge (Appendix 1). The questionnaire provided for asking the same questions systematically so that statistical analysis could be performed to summarize the data. Since hunting is illegal, we used a series of indirect questions, and crossed confirmatory questions, on the subject to minimize any bias associated with responses about conducting illegal activities. We asked the same question in two or more different ways to see if the response varied, especially about hunting which is a sensitive issue in some communities. For example, we asked both if there was hunting around the community and how many people in the community were hunting.

In addition to the interview questions, we constructed a matrix for a subset of pre-selected species, which we filled in with data on: 1) when was the last time the species was seen, 2) if it was hunted, and 3) why it was hunted. Eleven species were selected to be used in the matrix based on several criteria: 1) species known to be rare and/or elusive (Jaguar *Panthera onca*, Puma *Puma concolor* and Baird's Tapir *Tapirus bairdii*); 2) species known to be common (Central American Agouti *Dasyprocta punctata* and Mantled Howler *Alouatta palliata*); 3) species whose abundance was unknown (White-tailed Deer *Odocoileus virginianus*, Spider Monkey *Ateles geoffroy*i, Red Brocket *Mazama temana*, White-lipped Peccary *Tayassu pecari*); and, 4) species known to be hunted (Spotted Paca *Cuniculus paca*, Collared Peccary *Pecari tajacu*). The purpose of this matrix was two-fold: 1) to test the answers against similar questions in the interview which were open ended, and 2) to compare against data obtained in the camera-trap survey. In addition, by knowing more about how frequently species were seen and when was the last time they were seen, we hoped to gather information on temporal trends over the study area over the past 20 years.

Species diversity and relative abundance

Species abundance and diversity data were collected in CBTC from January 2005 to December 2006 during a camera trap survey of medium and large mammals (Chapter 2, this thesis). We subsampled capture data from the greater Talamanca region to only include those cameras deployed within the CBTC. Therefore, we summarized data from 130 camera-trap locations that were deployed at 8 different sites; those five used for the interviews and also Cahuita National Park (CNP), Hitoy-Cerere Biological Refuge (HBR) and Cordillera Costeña Talamanca (CCT) (Figure 3). As we were unable to deploy cameras in the Coroma community due to logistical difficulties, we made inference based on camera trap data collected from a nearby community (Yorkin, YOR) in the same indigenous reserve as a means of comparison.

Camera-trap data were analyzed individually to summarize species occupancy data per camera location and aggregated into sites based on proximity, which was defined by spatial overlap with interview locations. There are numerous ways to aggregate camera-trap data to estimate species richness and diversity across multiple locations. We used two methods: 1) summing the data per site (i.e. total); and, 2) averaging the data per site. Each of these methods has advantages and disadvantages, however, an average, or arithmetic mean of multiple samples can help to accommodate analysis in situations where there is uneven sampling among sites. To calibrate for differences in sampling effort among sites, we calculated trap success as a measure of relative abundance of species per site. Trap success (TS) is defined as the number of captures per 100 trap nights (calculated per sites as TS=total captures/trap nights*100), a method which accommodates variation in length of deployment (Kelly and Holub 2008).

To evaluate the number of species present at any given site, we calculated species richness (S). When data for locations were summarized into aggregate sites, both total species richness (S^t) per site (area) and average species richness (S^a) of all camera-trap locations ina an area were calculated. Because sample sizes vary among sites in this study, S^a is potentially a more robust method of comparison among sites, while S^t is more appropriate for identifying individual species presence/absence per site in order to evaluate covariates such as hunting, which often has species specific impacts (where one or more species are targeted).

Diversity indices are measures of species diversity in a defined species community (or site) and provide additional information on community composition. To estimate species diversity we used two common indices, Simpson’s index (D’) (Simpson 1949), which measures the probability that two randomly chosen individuals will be of different species, and Shannon’s index (H) (Shannon and Weaver 1949), which combines both species richness and abundance using information theory. We calculated H among sites, but not among species because when it is used to compare among species, it only measures the information content of non-zero values. However, when comparing among sites, this value is an expression of the diversity of species in each site. We calculated D’ for both sites and species. For sites, much like H, this value is an alternative index of the diversity of species in the sampling unit. In addition, we used both first order (Heltshe and Forrester 1983, Palmer 1990) and second order jackknife estimators

(Burnham and Overton 1979, Palmer 1991) by calculating the species-area curve with a Chi-Squared distance measure. These are nonparametric resampling procedures to estimate the true number of species in a sample. Diversity indices and analyses were done using PC-ORD software (MjM Software, Gleneden Beach, Oregon, U.S.A.).

Evenness (E) is a measure of the uniformity of species relative abundance among sites, which we calculated by dividing Shannon's index (H) by the natural log (ln) of richness (S) (Pielou 1969). We measured E both among species and sites. At the site scale, E is a measure of how evenly species relative abundances are distributed among the sites and is a useful means of comparing community structure. When comparing among species, E measures how consistently a species' relative abundances are distributed across all camera-trap locations in the study area. To aggregate camera-trap location data to do site scale analysis, we used the average E among locations contained within the site. The closer the value of E is to 1 the more evenly species are distributed. For example, a species with a value of 1 occurs in relatively equal proportion across all sites, while a species with a value of 0 would signify that there is only one occurrence record at one site.

We used analysis of variance (ANOVA) to evaluate relationships among trap success and evenness (E) among species and sites and to determine if there was a significant relationship between species community composition and relative abundance among sites.

Results

We were not able to distinguish indigenous from non indigenous ancestry during the interview process as too many of the families are mixed, especially in the BBV community; however, 22 of the people interviewed live within an indigenous territory. The average length of time respondents had been living in Talamanca was 25±1.29 years (range 3-67, n=91). All respondents gave the same duration for both 1) number of years residing on their property and 2) number of years in the Talamanca area.

Almost all respondents (98.9%, n=98) had noticed a change in the quantity of wildlife in the last 10 years, while one person did not know if there had been a change. When asked if the number of animals had either increased or decreased, 69% (n=69) gave responses indicating that animals were declining, 24% (n=24) gave responses indicating that animals were increasing, while 6% (n=6) did not express an opinion. Of the 24 people who responded that species were increasing, 23 were from the Bribri/Buena Vista Community. The reasons given by those respondents were that hunting had declined [83.3% (n=20)], that people had placed their properties in ESP and such a program protected species [16.6% (n=3)], and that MINAET (the ministry of the environment) prohibited hunting [8.3% (n=2)]. Perceptions varied of why species were declining, and we have only summarized the most frequent responses. Of those that responded that species were declining, 82.6% (n=57) indicated that hunting was a factor, 27.5% (n=19) that deforestation was a factor, 17.4% (n=12) that growth of human populations was a factor, and 2% each mentioned banana plantations and pollution as factors.

Human-wildlife conflicts

In order to understand what kind of domestic animals people had on their farms, we asked them to answer yes or no to a list of 9 options (see Appendix 1). Most interviewees responded (n=89) and indicated that they had anywhere from 0 to 8 different types of domestic animals on their farms (mean = 3.3 ± 0.19). The most common domestic animals kept on farms were chickens (n=76), dogs (n=68), pigs (n=51), horses (n=48), cows (n=38), and cats (n=32). Of the respondents, 22.4% (n=20) did not have any domestic animals.

Of the respondents who had domestic animals (n=75), 44% (n=33) said that wild cats or other wildlife had attacked their domestic animals within the last 10 years, while 56% (n=42) had not had any conflict with wildlife. Similar proportions said that other people in the community had problems with wildlife conflict (45.5%, n=36 said yes; 54.4%, n=43 said no). However, the majority of respondents (68.4%, n=52) did not think that wildlife conflict was a major problem in their community. Of those people responding that their domestic animals had been attacked by wildlife (n=54), most (64.8%, n=35) said that the attacks occurred more than once a year while the remaining respondents did not know how many attacks occurred. Of those that could provide an estimate (n=35), 74.2% (n=26) had more than three attacks per year and 22.8% (n=8) had more than 5 attacks per year on their farms. The majority of respondents said either that problems with human-wildlife conflict had not changed in the past 10 years (29.3%, n=17) or had decreased (27.5%, n=16), while 15.5% (n=9) said there had been an increase in conflicts.

Hunting

Most respondents, 92% (n=92), said that there was hunting around their community, while only 7% (n=7) said there was no hunting. When asked if they had noted changes in hunting frequency over the last 10 years, of those that responded (n=94), 19.1% (n=18) said it had increased, 29.7% (n=28) said it was the same, 47.8% (n=45) said it had decreased and 3.2% (n=3) said they did not know.

When asked how many people in each community were hunting, all 99 interviewees responded; 43% said 1-5 people, 28% said 5-10 people, 3% said 10-15 people, 8% said more than 15 people, and 17% said they did not know. The community most often referenced as having the most hunting was BSC (n=23). People hunting within a community can come from either inside or outside that community: 37.1% (n=36) of respondents (n=97) said hunters were from both inside and outside the community; 28.8% (n=28) said hunters were only from other communities; 23.7% (23) said hunters were only from their community; and, others did not know where the hunters came from (n=10).

There are a variety of reasons why people hunt. When asked if reasons were economic, subsistence or sport, the plurality (45.7%, n=43) thought hunting was done for both economic and subsistence activities, while the second highest proportion of responses indicated that it was only for subsistence reasons (26.6%, n=25). Only 9.5% (n=9) thought hunting was done for purely economic reasons, and 6.5% (n=6) thought each of the following were the primary reasons for hunting, only for sport, subsistence and sport, and all three (subsistence, economic and sport). Five people did not respond to this question.

The plurality of respondents (43.8%, n=32) were either not willing to answer or did not know how often they ate wild meat, while 24.6% (n=18) said they ate wild meat less than 5 times a month. One respondent ate wild meat over 15 times a month, and 30.1% (n=22) said they never ate wild meat. When asked where the wild meat that they ate came from, we received answers from 39 individuals (note that this is more than the number who said they ate wild meat in a previous question), 43.5% (n=17) of respondents got wild meat from hunting, 35.8% (n=14) received it as a gift, and 20.5% (n=8) bought the meat.

The favorite meat of those interviewed was pork (n=24), Spotted Paca (n=24), and domestic chicken (n=23). Surprisingly, few people said they preferred other commercially available meats: beef (n=1); fish (n=3); or rabbit (n=1). However, many people cited other wild meats as their favorites such as White-tailed Deer (n=9) and Collared Peccary (n=3). Other species mentioned at least once included Baird's Tapir, Geoffroy's Spider Monkey, Red Brocket, White-lipped Peccary, Green Iguana (*Iguana iguana*), Great Curassow (*Crax rubra*), and Great Tinamou (*Tinamus major*). Some respondents said they ate all types of meat (n=10).

Protected Areas

Our results indicate that local perceptions towards protected areas were generally positive, with 86.2% (n=75) of the respondents saying that protected areas benefit local people and only 13.8% (n=12) saying they did not benefit people, (13.7%, n=12, did not reply). In addition, 87.7% (n=79) of the respondents said they thought that protected areas helped to protect wildlife, while only 12.2% (n=11) said animals did not benefit, (10.0%, n=9, did not reply). However, the majority of respondents, 71.2% (n=62) did not think that the current reserve system was sufficient to protect wildlife, while 28.7% (n=25) though the protected areas network was sufficient, (13.7%, n=12, did not reply). Finally, of those people interviewed, 89.4% (n=85) said that they lived near a protected area, while 11.1% (n=10) said they did not live near a protected area, (4.4%, n=4, did not respond). Since all residents of the CBTC are close to some form of protected area, this response signifies an ample understanding of surrounding public lands.

Species matrix

Responses to when each of the eleven species in the matrix was last seen varied among species (Table 1) and communities. Only ten people reported ever seeing a White-lipped Peccary, six within the past five years and four more than 20 years ago. Of the six respondents who had seen this species in the last five years, three were from COR and three from BSC. Of the four who had seen it over 20 years ago, two were from COR and two from BBV. Baird's Tapir was also rarely reported, with 61.9% (n=13) of the respondents who had ever seen the species saying they had not seen one in over 20 years.

We also evaluated where globally-threatened species were last seen by respondents to the interviews (Table 2). Both respondents who had seen Baird's Tapir in the last 5 years were from BSC; however, over 20 years ago it was frequently reported as far east as GAN. In addition, the Geoffroy's Spider Money was seldom reported more than 5 years ago, but has since been seen in BBV, BSC and KEK. The Red Brocket had been seen consistently in BSC over the past 15 years, but was also seen in BBV in the past 5 years. Many of the threatened species had been recorded in COR, BBV and BSC recently, and none of these had been seen in GAN in over 20 years.

When asked which species from the matrix were hunted often, most respondents indicated Spotted Paca, Collared Peccary and White-tailed Deer, and respondents said they rarely take Central American Agouti (Table 3). The species most frequently mentioned as not being hunted was Mantled Howler Monkey, but also frequently mentioned were Jaguar, Puma and Geoffroy's Spider Monkey. The only species mentioned as being taken for economic reasons is the Spotted Paca. For subsistence use, there was a preference for Spotted Paca and also Collared Peccary, Central American Agouti, and White-tailed Deer. Few respondents mentioned hunting for sport; however, Bairds' Tapir was mentioned once and is a known target of sport hunting on the Pacific slopes of the Talamanca.

Species abundance and diversity

Camera-surveys recorded 1315 capture events (photographs) containing species over a 14-month period. We used data from 130 camera-traps. Of these, 19 did not take any photographs, and we excluded data from another 29 cameras that were spatially redundant (i.e., where 2 cameras were in the same location). Ultimately, we present the data from 82 camera-trap locations over a period of 3,582 trap nights (24-hour periods).

We photographed 28 species in total, 21 species of terrestrial mammals, 2 primates, and 4 birds. One photograph of an iguana was taken but not used in the analysis. Thus for each of the 27 species used in the analysis, we calculated summary statistics and measures of diversity. Using a species-area curve, we estimated that there could be as many as 30.0 (First-order jackknife) to 31.9 (Second-order jacknife) species total, suggesting that with further effort we could possibly find 3-5 more species. Three species were only captured once (n=1): Mantled Howler Monkey, Greater Grison, and Central American Red Brocket. Four other species were captured fewer than 10 times: Jaguar (n=2); Jaguarundi (n=4); White-throated Capuchin (n=4); and, Gray Four-eyed Opossum (n=8). The birds captured included the Great Currasow (n=53) and the Grey-chested Dove (n=36). The Central America Agouti was, by far, the most frequently captured animal (TS=13.36), followed by White-nosed Coati (TS=4.61), Nine-banded armadillo (TS=2.96), and Black-eared Opossum (TS=2.60) (Appendix 2).

Trapping effort was not equal among sites and ranged from 168 trap nights in GAN to 725 trap nights in BBV, however trap nights were not significantly correlated to average richness (R^2=0.00, p=0.97), Simpson's diversity index (R^2=0.00, p=0.99), Shannon's diversity index (R^2=0.00, p=0.908), or evenness (R^2=0.01, p=0.814). Total richness however was correlated with trap effort (R^2=0.73, $p<0.05$). The lack of consistent effort per site is due to two primary factors, 1) camera theft and 2) site accessibility. We lost 4 camera-traps due to theft in GAN (and subsequently abandoned the site), 5 in KEK, and 1 in CNP. Trap success varied from 44 to 22 captures per 100 trap nights among the eight sites; however, half of the sites (HBR, YOR, KEK and BBV) had trap success greater than 40 captures per 100 trap nights (Fig. 4). The lowest trap success was CCT (TS=22.38, Table 4).

Species relative abundance varied among sites, with some species only being found at one or two sites while others occurred across all sites. BBV was the site with the maximum relative abundance for many of the larger "landscape" mammal species, in particular Jaguar, Puma, and Collared Peccary (Table 5). HBR was the only site containing Central America Red Brocket, and this was also the site with the highest relative abundance of the most common small mammal, Central American Agouti.

Species richness was measured using both the sum of all species captured per site (S^t) and the average richness among the individual camera-traps per site (S^a). Total species richness was highest at BBV ($S^t = 19$) and BSC ($S^t = 17$), while those locations with the lowest total richness were GAN ($S^t = 10$), CCT ($S^t = 11$), and YOR ($S^t = 14$) (Fig. 5). Average richness showed a slightly different pattern and may be a more robust measure of richness in studies where trap nights vary among sites, as it is independent of effort. Average richness was highest in YOR ($S^a = 6.0$), followed by BBV ($S^a = 5.40$) and BSC ($S^a = 4.75$), while the lowest averages were CCT ($S^a = 3.50$) and CNP ($S^a = 4.21$).

Sites with the most evenly distributed species communities (lowest average E across all camera-trap locations) were COR (E=0.87), BBV (E=0.81), BSC (0.79), and KEK (E=0.78). Sites with the least evenly distributed species communities were CNP (E=0.67), CCT (E=0.71), GAN (E=0.71) (Fig 6). Using Shannon's index (H) and averaging all camera locations per site, the site with the highest diversity value is COR (H=1.54), followed by BBV (H=1.30) and BSC (H=1.21), while the lowest values were observed in CCT (H=0.93), CNP (H=1.03), and GAN (H=1.08). Simpson's index (D) showed similar patterns.

Discussion

Interviews provided us with a means of gathering data on perceptions of wildlife, human-wildlife conflict and wildlife use issues across the CBTC. Social data is very important to help guide planning for species recovery and management outside of protected areas as it gives an indication of acceptable outcomes for species conservation efforts, provides an indication of tolerance to species targeted for recovery, and contributes information on the potential to curb illegal activities such as hunting.

Are protected areas enough to conserve mammals in the CBTC?

Protected areas are an important component of the CBTC yet, in most cases, are completely surrounded by a human-dominated landscape. It is therefore very important to understand perceptions of these areas among the communities that live around them. The majority of respondents (86%) had positive opinions of protected areas and said that they benefit local communities, and a similar number also recognized the value of protected areas for protecting wildlife. Interestingly, over 70% of the respondents did not think the current reserve system was sufficient to protect wildlife species.

The distributions of mammals and terrestrial birds in the human-dominated landscape outside the protected areas in the CBTC are heavily influenced by the combined effects of habitat alteration and illegal hunting. Terrestrial mammal community diversity in the CBTC is composed of a high proportion of carnivores, especially felids (Fig. 7). Among the felids Margay and Ocelot were by far the most abundant, occurring in almost every site sampled. Both of these species are tolerant of human disturbance, however, they remain confined to remnant forest fragments. Neither of these species was abundant where Puma and Jaguar were present (BBV), and thus their predominance could be attributed to a trophic cascade effect where, in the absence (or rarity) of large predators, mesocarnivore populations increase. However, further research is needed to explore this hypothesis.

Although trap success, species richness and diversity were relatively high in protected areas within the study area, the site with the highest “value” for mammal conservation was BBV, a private conservation area. BBV was the only site with large cats (Jaguar and Puma) and also had the highest total species richness. This finding clearly demonstrates the value of this property for the persistence of large mammals and the need to ensure its long-term protection. On the other hand YOR, within the BriBri Indigenous Territory, had the highest values for average species richness and diversity, and the second highest trap success. This suggests that the potential for large mammal conservation on Indigenous lands is high, and such lands should be a focus of future conservation efforts. Among the existing protected areas in the CBTC, HBR was the most intact based on mammal fauna. HBR has the highest trap success among all the sites, and it the only site where Central American Red Brocket was found. Although CNP was the only site where several primates were photographed, trap success and species diversity were relatively low and several cameras were stolen from this site indicating a strong human presence.

Based on the combined findings from camera-trapping and local interviews, we suggest that protected areas alone are not sufficient to conserve large mammals in the CBTC.

Is there a relationship between hunting and wildlife abundance and diversity?

Almost all interviewees have noticed a change in wildlife abundance in the last 10 years, the majority citing a decline in visible abundance. Almost all of the respondents who indicated species were increasing were from the same community (BBV), citing that hunting had declined and that properties were entering into ESP programs that prohibited hunting. Based on these responses, it is clear that local people make a connection between hunting and wildlife abundance and the effects of overhunting on wildlife. BBV was identified via the interviews as the site with the greatest decline in hunting, and this corresponded with its high total species richness and abundance of large carnivores, as determined via camera trapping. BSC, the site most often referred to as having the greatest hunting by interviewees, exhibited much lower species richness and relatively low diversity compared with BBV, even though the two communities are in close geographic proximity.

What impact does wildlife conflict have on mammal populations?

It is difficult to measure the impact of retaliatory killing on wild mammal populations. The vast majority of the interviewees keep domestic animals on their farms. Less than half of the respondents reported having conflicts between their domestic animals and wildlife, and a similar number reported that other community members have wildlife conflict problems. However, even though many people had their domestic animals impacted in some form by wildlife at least once a year, the predominant perception is that wildlife conflict is not a major problem in their communities. Based on the answers of those that responded to the question, wildlife conflicts do not seem to be increasing in most communities, but are either similar to past years or diminishing.

Although people do not perceive wildlife conflicts as a major problem in their communities, there is a noticeable lack of any large carnivores from all but one site. Because neither Jaguar nor Puma are commonly hunted, it is possible that their absence from most sites could be related to a perceived threat by some residents. However, the fact that Jaguar and Puma relative abundances correspond to that of Collared Peccary suggests that available prey might also have an influence on their persistence. During our study one Puma was killed in retaliation for eating a domestic goat, indicating that wildlife conflict, perceived or otherwise, could be one of the limiting factors to the persistence or large carnivores in the CBTC. This suggests that community education and outreach activities about large carnivores within the villages that border BBV and elsewhere might be necessary for the long-term survival of large carnivores in the corridor.

What impact does hunting have on mammal populations?

The majority of large-scale deforestation in the CBTC occurred historically, and what remains today is a relict of the banana and cacao booms of the mid-1900's. Hunting, however is a persistent threat to many species and one which is difficult to quantify and even more difficult to prevent. The impacts of hunting on wildlife vary among areas and among species. In general, the larger mammals most often sought after by hunting have disappeared from human-dominated areas, but persist in low numbers in peripheral protected areas and private conservation areas. Even the most sought-after mammal, the Spotted Paca, still occurs in all but the most heavily hunted areas, albeit in increasingly low numbers.

Nearly all interviewees recognized that there is hunting in their communities, but the majority of respondents said that hunting had decreased over the last 10 years. Although data from the camera-traps does not have a temporal component, the heterogeneity in species occupancy among sites suggests that hunting is having an impact on some species in areas of high human influence. Generally, people reported that fewer than 10 people were hunting in the community and that hunters came both from inside the community and from elsewhere to hunt. This suggests that although hunting has declined within the CBTC, it is still prominent in some areas. Interestingly, several interviewees suggested that the increase in access to electricity and ultimately televisions has been one of the primary causes in the reduction of hunting, especially over the weekends when soccer games are aired.

One community in particular (BSC), was often referenced by surrounding communities as having the most hunting. This community, however, did not show the lowest trap success and diversity. This could be due to the effect of communities (BBV and HBR) that border BSC acting as source populations for some species. The community of GAN, by contrast is almost completely surrounded by banana plantations and a major highway. With a potentially low recruitment of new mammals, hunting in GAN is likely to have greater impact as suggested by the very low trap success and diversity we observed via camera trapping.

Most respondents said that local hunting was done both for economic and subsistence reasons or for subsistence alone. When asked if they consumed wild meat, most respondents declined to answer, presumably due to the fact that hunting is illegal. Of those that said they did eat wild meat, the majority was from hunting, but it was reported as obtained either as a gift or purchased. When asked what meat was their favorite, an equal number responded that pork and Spotted Paca were their favorites, suggesting that Spotted Paca was most likely targeted for hunting for that reason. Spotted Paca was indeed the species most often cited as being frequently hunted both for subsistence and for economic reasons. On several occasions meat from this species was seen being sold (illegally) in supermarkets in the region. Spotted Paca has the greatest relative abundance in the YOR, followed by BBV and KEK. We would expect to find high abundance in BBV, as it is the site with highest conservation value for mammals, however the abundance of this species in Indigenous Territories might be unexpected. However, since indigenous people more commonly hunt for subsistence and, therefore, do not target any species in particular as commercial and sport hunters do, Spotted Paca have a higher probability of survival in the Indigenous Territories. Based on this information, Spotted Paca is also an indicator species for sites with high non-subsistence type hunting. This pattern would partially explain the rarity of the species in BSC and surrounding areas that have the greatest number of hunters and the absence of the species from areas with high hunting and little remaining habitat (GAN and CCT).

Often mentioned as other favorite food items were White-tailed Deer and Collared Peccary, although many people said they eat all types of meat. Not surprisingly, both of these species are cited as being often hunted, and thus we can see a pattern emerging between responses to people’s favorite meat and species targeted for hunting. Interestingly, we never recorded White-tailed Deer during any of our surveys, suggesting that it has either been overhunted and/or that it prefers non-forested habitats. Although White-tailed Deer was not found in this study, another study in the same area did record the species from more open habitat (Harvey et al. 2006), suggesting that we did not capture it because we only sampled closed forest areas. Collared

Peccary was found in only three sites, and was most abundant in areas with some type of protection (HBR and BBV).

In general, the vast majority of large mammals are missing or very rare in the study area. In order to understand the spatial and temporal context of these vanishing large mammals, we can examine when and where the last time these animals were seen. Also, in order to better understand the impacts of habitat loss over time versus current hunting patterns, it is important to have a historical context. For example, we never recorded White-lipped Peccary during our surveys even though it was reported as a favored food item. Of all the respondents, only 10 people had ever seen one, 6 in the last 5 years and 4 over 20 years ago. In contrast, over 21 people reported having seen Collared Peccary in the last 5 years. In addition, although we never recorded Baird's Tapir, 2 people have seen one in the last 5 years, while 13 people had not seen one in over 20 years. This finding suggests that these species, as well as others, were historically much more common than our current data suggests.

We can, therefore, discern that hunting has a negative impact on mammal presence and abundance, but that hunting alone does not explain the current distribution of species. We have very limited information on historical context, but based on present knowledge species that are currently rare or absent were more common in the past. Our data also suggests that different types of hunting have different impacts, species-targeted hunting (especially for Spotted Paca and Collared Peccary) can cause local extirpations, while subsistence hunting tends to have less visible impacts on mammal abundance and diversity.

Summary

Species diversity and relative abundance varied greatly among sites, as did community structure. Determining the cause of these variations and the effects of numerous potential explanatory variables is a daunting task. Although our camera–trap sampling was fairly extensive, our efforts were confined to forested areas within and around the human dominated landscape, thus there is a high probability that with continued effort we would find additional species not recorded during this study, albeit in low numbers. Of the species we did not capture, we suspect that sampling in open grassland habitat would increase our chances of trapping White-tailed Deer, for example, which were recorded within the CBTC by Harvey et al. (2006).

Our study suggests that while hunting alone is not responsible for the current distribution and abundance of medium and large mammals, it is one of the limiting factors influencing the future persistence of many species. Human-wildlife conflicts may also have a negative impact, both on the perceptions by local residents of the value of wild mammals but especially on the long term persistence of large carnivores. If the conservation of Jaguar and Puma is a priority, then working with local people to both improve livestock pens and reduce hunting of prey species must go hand in hand. Hunting of Central American Red Brocket, both Peccary species and other prey items required to sustain large carnivores likely has an indirect negative impact on livestock by increasing their mortality from carnivore attacks. Reducing hunting by individuals therefore would have a long-term benefit for human livelihoods across the region.

Conclusions

The CBTC is designed to connect La Amistad NP and the mountains with the coastal zone and coral reefs. The majority of large mammals have disappeared from the CBTC, but many are still present in La Amistad NP. However, there currently exists the opportunity to conserve the large mammal faunas missing from much of the lowlands in Indigenous Territories, private conservation lands and protected areas. Conservation in Indigenous Territories and private lands will require education and outreach at the community scale to promote the perceived value of wildlife. Both tourism and environmental service payments offer financial incentives to conserve mammals. The CBTC is in a unique position to help encourage these efforts.

The success of the CBTC in restoring habitat and wildlife populations depends almost entirely on the residents of the region, since a majority of the planning area is privately owned. Our data suggest that human views of protected areas and species conservation are very positive and that local knowledge of both the current and historical context of wildlife is robust. Residents are aware that hunting is a problem and that it is causing a decline in abundance of species, but feel that they cannot do anything about it, as often the people illegally hunting are part of their community.

Wildlife conservation need not be mutually exclusive of regional development and human prosperity. In fact, in the CBTC wildlife viewing is a source of revenue from tourism, especially in the protected areas and private wildlife refuges. Tourism is a major industry in the area, however, the benefits from it do not always trickle into the rural sections of the corridor where other mechanisms are needed to promote conservation of private lands. The value of private lands for conservation in the CBTC cannot be overstated, as the connecting sites needed among forests fragments are all on private property. Harvey et al. (2006) reported on the importance of agroforestry areas for mammal diversity in the Talamanca region and the potential to include trees and crops has been explored in many traditional agricultural systems. The CBTC currently manages a nursery and promotes reforestation around the region. An emphasis on growing native trees that benefit wildlife (fruiting trees, etc.) could be an important step, especially in establishing viable movement corridors for biodiversity.

There is one inconsistency in our dataset that could indicate a weakness in using interview data to evaluate hunting. Although our ranking system of hunting intensity per site placed BSC as being less hunted than BBV, almost all of our species data suggest otherwise. The reason why this discrepancy occurred is clear, but the means to fix it is less clear. The species data were collected from camera-trapping where our probability of capture is highly dependent on trap placement, which is partly reflective of site selection. In BBV we were granted permission to use the ACODEFO site for camera-trapping, but securing permissions elsewhere in the study site proved difficult. In BSC there were no large properties, and thus we were able to work with the community to access many private properties. Therefore, although the BBV site might have more hunting, we trapped in an area that was partially sheltered from this impact as it was protected by the CBTC. In contrast, in BSC where there is less hunting, we focused our trapping on private lands where there is no protection or enforcement. We recognize this potential inconsistency, but after accounting for this the results do not change substantially, and thus our conclusions remain well founded.

In addition, site access is also a significant problem when working on private property, and, in most cases, a camera-trap network must span several properties and can be limited by the willingness of the owners to cooperate. Access to the BriBri and Cabécar Indigenous Territories was at the discretion of the elected officials, which change periodically. Access to protected areas is at the discretion of MINAET, however, so we retained permits throughout the study period and had continuous access to all government-owned lands.

Hunting is likely the primary reason for the disappearance of the large mammal fauna from the CBTC. The disappearance of the Giant Anteater and White-lipped Peccary and the extreme rarity of the Jaguar, Baird's Tapir, White-tailed Deer, and Central American Red Brocket in the corridor are the consequence of a century of overhunting together with forest loss and infrastructure development (road-kill likely contributed to the loss of the Giant Anteater). We can infer from our interview data that most of these species were found here 10-20 years ago and, in fact, some were quite common until recently. We can also assume that, in the absence of hunting, White-tailed Deer would still be common, as they are habitat generalists and often benefit from the types of land use in the region, especially pasture for cattle farming. Local knowledge suggests that the Jaguar, Baird's Tapir, and White-lipped Peccary still do visit the region; however, it is most likely a population sink as none of these species persist here.

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Table 1: Responses to when the species was last seen (n=67). * are species that were never seen in camera-traps. “Tracks only” indicates that the species was not seen directly, but interpreted from tracks and is inferred to be elusive. “Year round” signifies that the species is seen throughout the year and is inferred to be common. ya= indicates years ago.

English name	**Local name**	***Scientific name***	Tracks Only	Year Round	<5ya	6-10ya	11-15ya	16-20ya	>20ya
Jaguar	Tigre, Jaguar	*Panthera onca*	19	0	9	3	1	0	4
Puma	Puma, Leon	*Puma concolor*	15	0	11	3	0	1	1
White-lipped Peccary	Chancho de monte	*Tayassu pecari**	0	0	6	0	0	0	4
Collared Peccary	Saino	*Pecari tajacu*	16	13	21	3	2	2	0
Spotted Paca	Tepezcuintle	*Cuniculus paca*	16	8	15	2	1	1	0
Baird's Tapir	Danta	*Tapirus bairdii**	0	0	2	1	4	1	13
White-tailed Deer	Venado cola blanca	*Odocoileus virginianus**	1	9	9	3	0	1	0
Red Brocket	Cabro monte	*Mazama temama*	5	3	4	1	1	0	0
Central American Agouti	Guatuza	*Dasyprocta punctata*	6	32	15	1	0	0	0
Geoffroy’s Spider Monkey	Mono arana	*Ateles geoffroyi*	0	10	3	0	0	0	0
Mantled Howler	Mono congo	*Alouata palliata*	2	32	4	0	0	0	0

Table 2. Globally threatened species on the 2008 IUCN Red List and the communities they were reported as seen near during the various time intervals reported in the interviews. BriBri/Buena Vista (BBV), Bocuare/San Rafael/Carbón (BSC), Coroma (COR), Gandoca (GAN), and Kekoldi (KEK). IUCN Red List of Threatened Species (2008) categories below are endangered (EN), near-threatened (NT) and data deficient (DD).

English name	**IUCN 2008**	**<5ya**	**6-10ya**	**11-15ya**	**16-20ya**	**>20ya**
Baird's Tapir	EN	BSC	BBV	COR BSC	BSC	COR BSC GAN
Geoffroy's Spider Monkey	EN	BBV BSC KEK				
Jaguar	NT	COR BBV BSC	BSC KEK	BBV		COR BBV
White-lipped Peccary	NT	COR BSC				COR BBV
Red Brocket	DD	BBV BSC	BSC	BSC		

Table 3. Responses to hunting frequency (n=38) and reasons for hunting (n=35) questions from the species matrix. Reasons for hunting depicted are economic (Econ), subsistence (Subsist) and sport.

	Hunting Frequency			Reason Hunted		
English name	**OFTEN**	**RARELY**	**NEVER**	**Econ**	**Subsist**	**Sport**
Jaguar	2	5	9	0	1	0
Puma	1	2	6	0	0	0
White-Lipped Peccary	3	4	0	0	6	0
Collared Peccary	13	16	2	1	26	0
Spotted Paca	20	11	1	9	28	1
Baird's Tapir	1	3	1	0	1	1
White-tailed Deer	8	6	3	0	11	1
Red Brocket	1	3	1	0	3	0
Central American Agouti	4	26	5	0	22	0
Geoffroy’s Spider Monkey	0	0	7	0	0	0
Mantled Howler	1	2	19	0	1	0

Table 4. Site analyses: Cam=number of cameras, TN=trap nights**,** S^t =total (sum) richness, S^a=average richness, D'= Simpsons diversity index, E=Evenness, H=Shannons's diversity index, BBV (Bribri/Buena Vista), BSC (Bocuare/San Rafael/Carbón), CNP (Cahuita National Park), YOR (Yorkin/Coroma), GAN (Gandoca Manzanillo), HBR (Hitoy-Cerere Biological Refuge), KEK (Keköldi), CCT (Cordillera Costeña Talamanca).

SITE			TRAP SUCCESS			CAPTURES			RICHNESS		DIVERSITY		
Name	Cam	TN	Sum	Mean	Max	Sum	Mean	Max	S^t	S^a	D	E	H
BSC	16	766	30.55	1.13	10.18	234	8.67	78	17	4.75	1.21	0.79	0.61
BBV	15	725	41.38	1.53	13.10	300	11.11	95	19	5.40	1.30	0.81	0.65
CNP	14	494	36.23	1.34	9.72	179	6.63	48	17	4.21	1.03	0.67	0.52
HBR	13	522	44.44	1.65	25.29	232	8.59	132	17	4.38	1.07	0.75	0.55
KEK	11	425	42.82	1.59	24.47	182	6.74	104	15	4.64	1.13	0.78	0.58
CCT	6	286	22.38	0.83	5.25	64	2.37	15	11	3.50	0.93	0.71	0.49
YOR	4	176	44.32	1.64	17.61	78	2.89	31	14	6.00	1.54	0.87	0.74
GAN	3	168	27.38	1.01	6.55	46	1.70	11	10	4.67	1.08	0.71	0.54

Table 5. Relative abundance of species among sites. N(t)=number of total captures of species, Max RA= Maximum relative abundance of species among all sites, Max Group= site with the maximum relative abundance per species, BBV (Bribri/Buena Vista), BSC (Bocuare/San Rafael/Carbon), CNP (Cahuita National Park), YOR (Yorkin/Coroma), GAN (Gandoca Manzanillo), HBR (Hitoy-Cerere Biological Refuge), KEK (Kekoldi), CCT (Cordillera Costena Talamanca). Species with * are birds

Common name	N(t)	Max RA	Max Group	BBV	BSC	CNP	YOR	GAN	HBR	KEK	CCT
Collared Peccary	37	65	BBV	65	7	0	0	0	27	0	0
Great Tinamou*	18	24	BBV	24	19	0	15	20	23	0	0
Jaguar	2	100	BBV	100	0	0	0	0	0	0	0
Puma	10	100	BBV	100	0	0	0	0	0	0	0
Rufous-necked Wood-Rail*	13	47	BBV	47	37	17	0	0	0	0	0
White-nosed Coati	165	34	BBV	34	12	11	21	0	8	9	5
Greater Grison	1	100	BSC	0	100	0	0	0	0	0	0
Nine-banded Armadillo	106	24	BSC	14	24	5	8	7	10	12	19
Striped Hog-nosed Skunk	29	39	CCT	4	15	12	0	11	15	3	39
Tome's Spiny Rat	13	53	CCT	0	40	0	0	0	0	7	53
Gray Four-eyed Opossum	8	67	CNP	0	0	67	33	0	0	0	0
Gray-chested Dove*	36	76	CNP	2	7	76	9	0	3	3	0
Mantled Howler Monkey	1	100	CNP	0	0	100	0	0	0	0	0
Northern Raccoon	86	42	CNP	0	8	42	0	8	0	11	31
Northern Tamandua	17	36	CNP	4	4	36	14	19	4	10	9
White-throated Capuchin	4	100	CNP	0	0	100	0	0	0	0	0
Black-eared Opossum	93	20	YOR	1	14	13	20	20	17	11	5
Jaguarundi	4	51	YOR	0	0	0	51	0	31	18	0
Red-tailed Squirrel	13	47	YOR	17	0	4	47	0	5	17	10
Spotted Paca	24	53	YOR	19	4	3	53	0	8	13	0
Tayra	22	68	YOR	11	13	7	68	0	0	0	0
Great Curassow*	53	56	GAN	27	10	0	0	56	5	0	3
Margay	30	23	GAN	16	15	10	0	23	3	22	11
Ocleot	33	63	GAN	8	0	1	5	63	18	5	0
Central American Agouti	482	22	HBR	14	11	3	17	7	22	21	5
Central American Red Brocket	1	100	HBR	0	0	0	0	0	100	0	0
Demarest's Spiny Pocket Mouse	14	42	KEK	10	0	0	19	0	29	42	0

Figure 1. Protected areas and Indigenous Territories inside and surrounding the CBTC (bold black lines). IT= Indigenous Territory, NP=National Park, BR=Biological Refuge, WP=Wildlife Refuge.

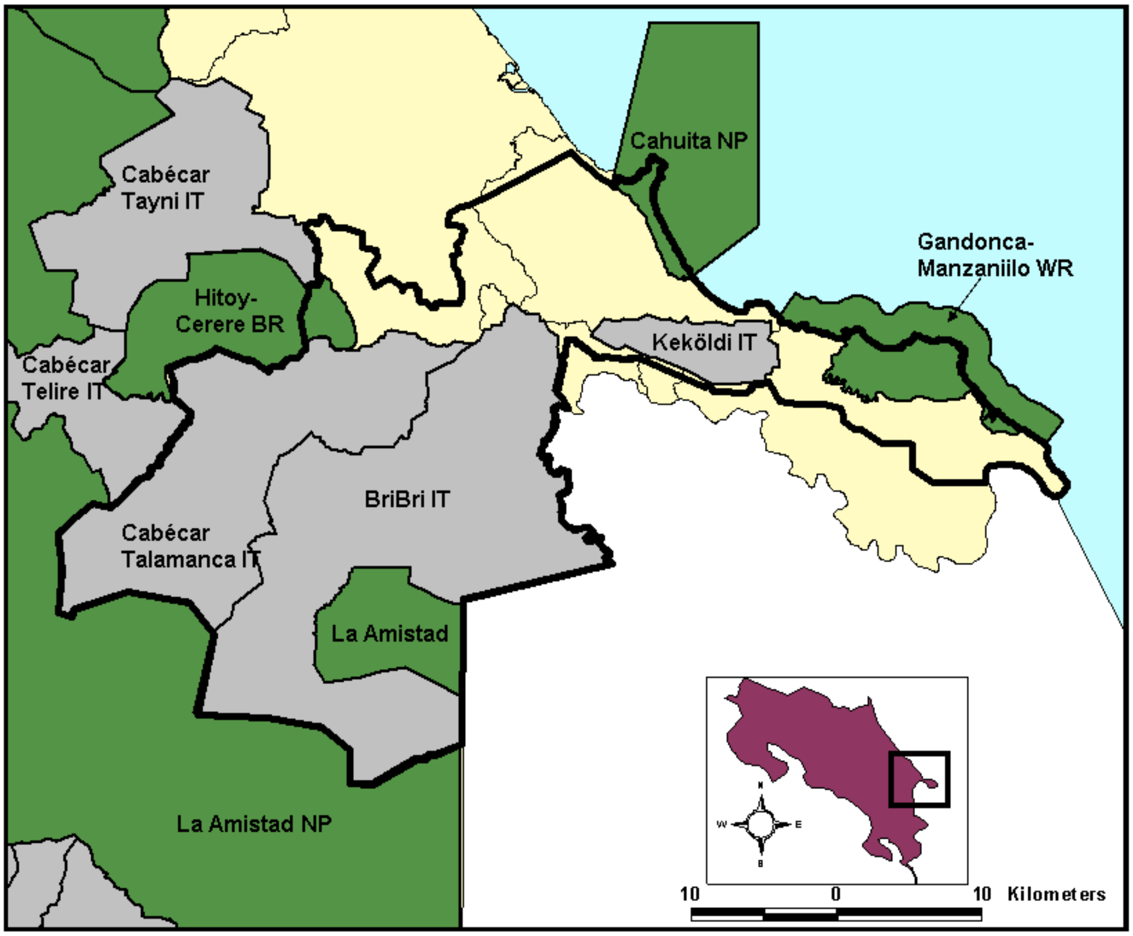


Figure 2. Map showing locations of interviews (red) and camera traps (yellow) with remaining forest cover.

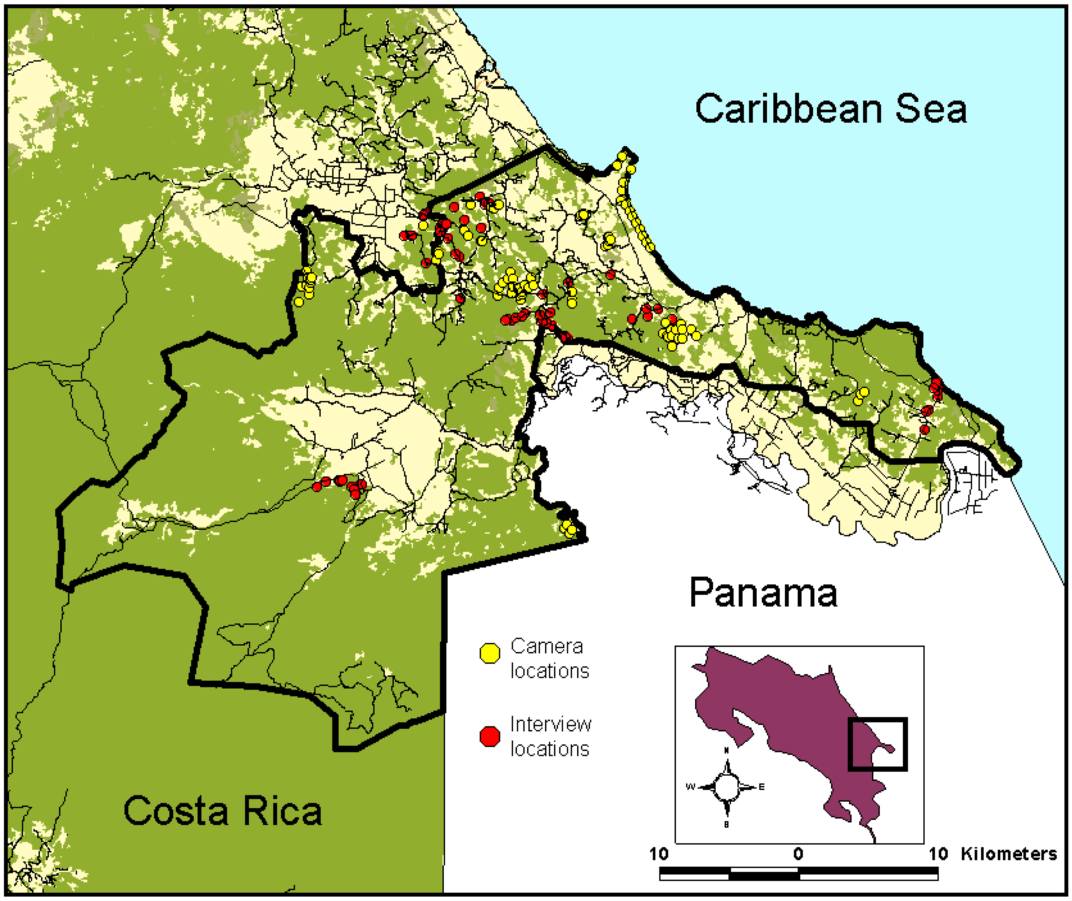


Figure 3. Sites where cameras trap were set and interviews were conducted; Bribri/Buena Vista (BBV†), Bocuare/San Rafael/Carbón (BSC†), Keköldi (KEK†), Gandoca (GAN†), Coroma (COR*), Hitoy-Cerere Biological Reserve (HBR**), Yorkin (YOR**), Cordillera Costeña Talamanca (CCT**), Cahuita National Park (CNP**). † camera-trapping and interviews, * interviews only, **camera-trapping only.

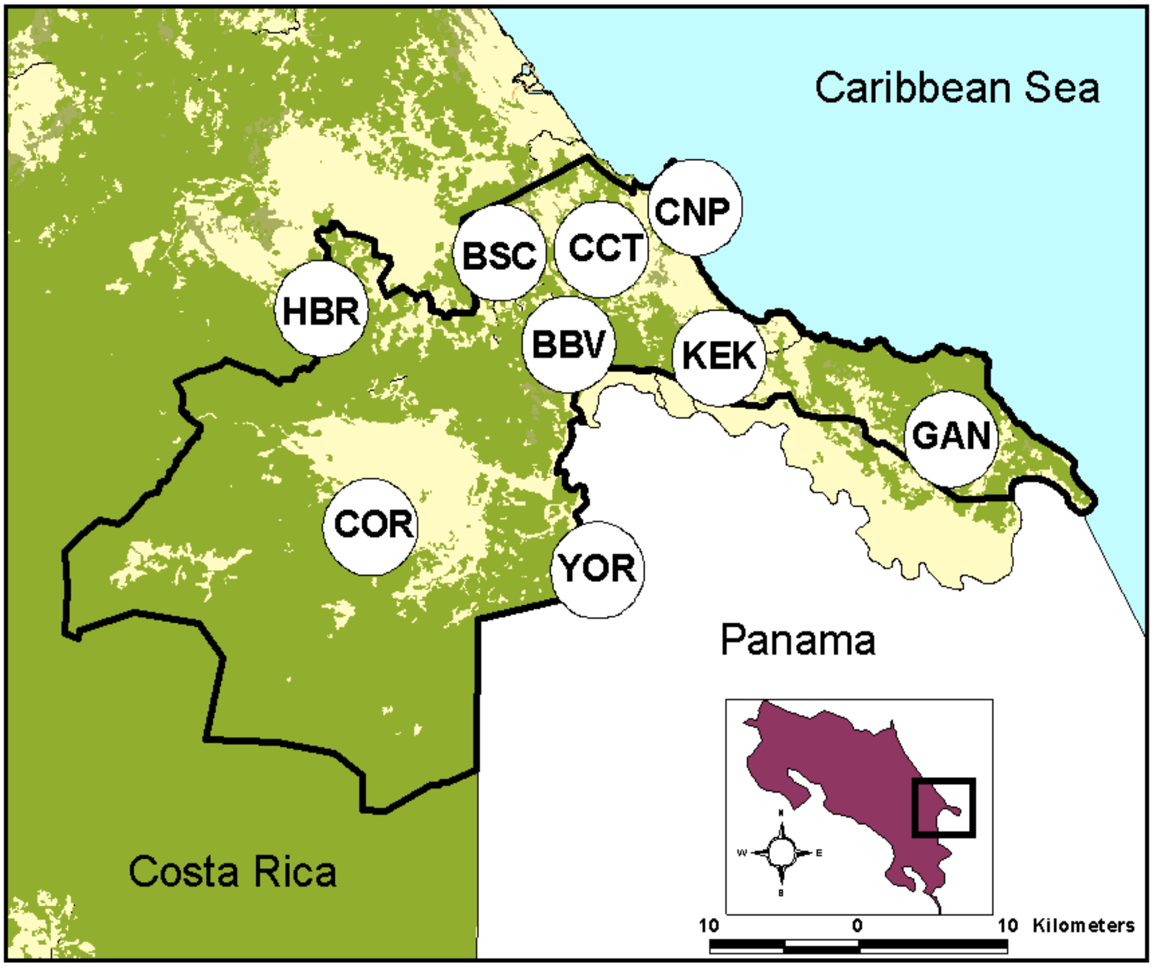


Figure 4. Sum of trap success* per site (+/- SE). Trap success=total captures/total trap nights x100.

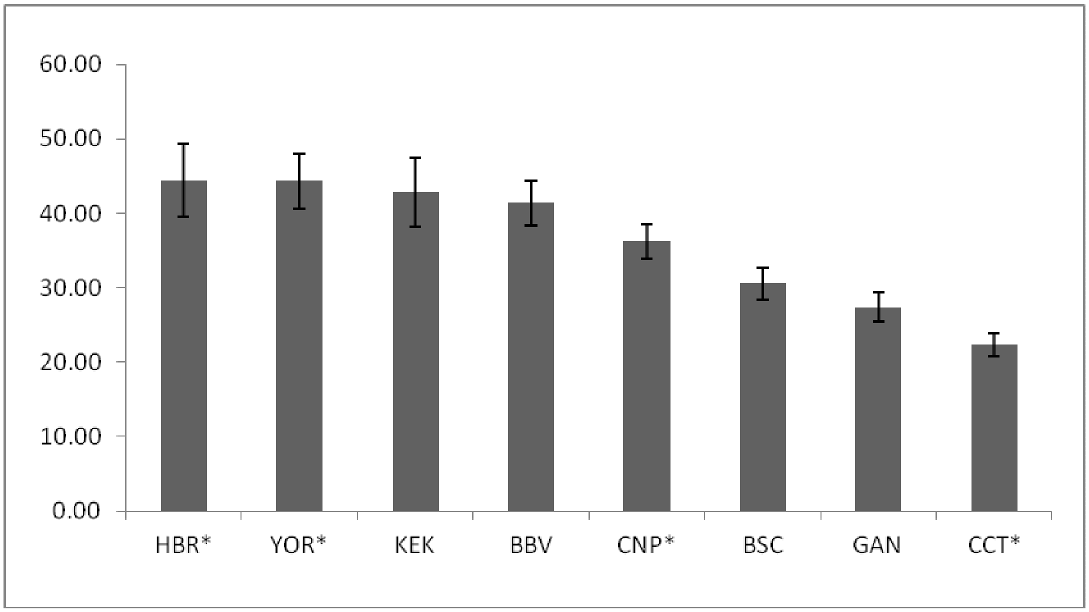


Figure 5. Average (Sa) and total (St) species richness between sites.

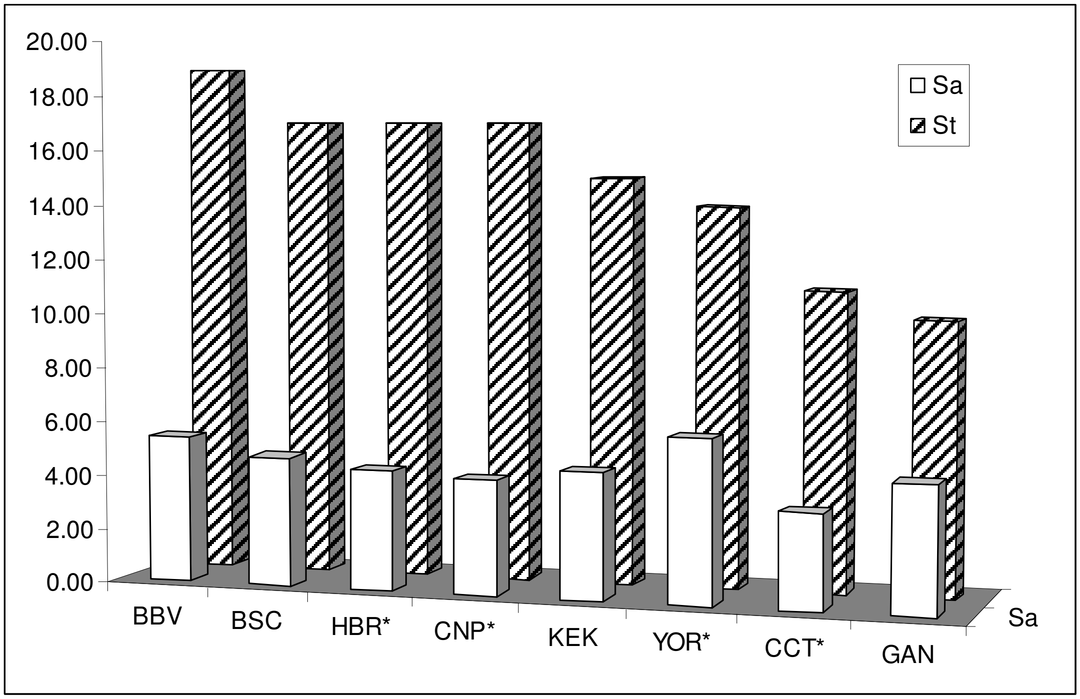


Figure 6. Graphic comparison of several diversity indices per site (D= Simpson's index, E=Evenness, and H=Shannon's index).

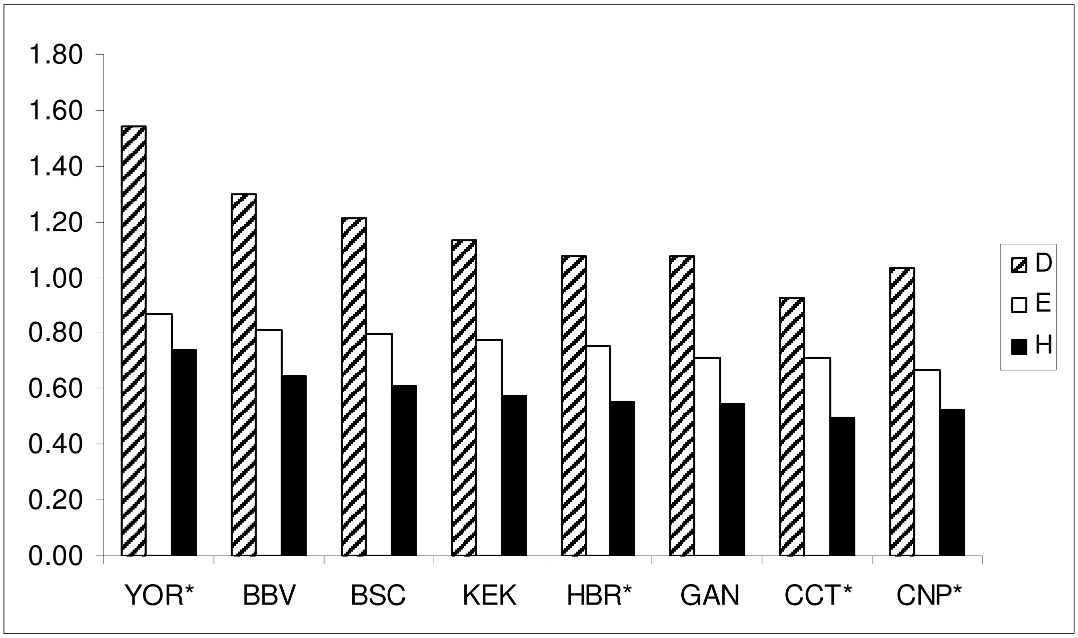
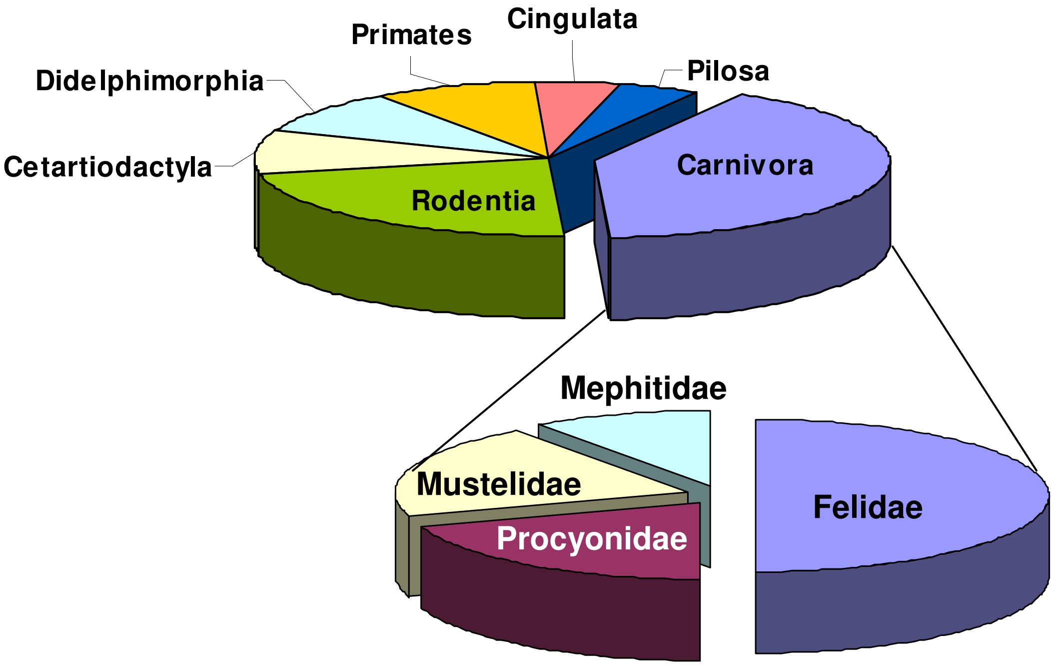


Figure 7. Relative percentage of mammalian Orders and Carnivore Families sampled for all species and for carnivores.



Appendix A: Interview Questions

Fecha:________/_______/200____
Comunidad____
Persona haciendo entrevista:_____________________________
Referencia (GPS): 17P__________, UTM ____________

1. Cual es su nombre? ______________________________________
2. Cuantos años tiene de vivir en la finca?_______________
   en Talamanca?______________

3. Ha notado cambios en la cantidad de animales silvestres en los últimos 10 años? En cuales especies ha notado cambios?

(han incrementado) __________________________________
(esta igual) __________________________________
(ha disminuido) __________________________________
(NO SE)

4. *Porque* piensa usted que esto ha ocurrido?

____
____

CONFLICOS ENTRE FELINOS y HUMANOS

5. Tiene usted animales domésticos en la finca? (Si o No)

Vacas____________ Chanchos______________
Pollos____________ Pavos________________
Caballos__________ Cabros________________
Perros___________ Gatos_________________
Otros:_______________________________________

6. (Si) Felinos silvestres u otros animales han molestado o han comido sus animales? (Si o No)

   Cuales animales, que felino y cuando?

7. (Si) Cuantas veces en un año hay ataques en su finca?
   (uno)
   (dos)
   (tres)
   (cuatro)
   (cinco)
   (mas que cinco)
   (NO SE)

8. Otras personas han tenido problemas con felinos molestando animales domésticos? (Si o No)

9. Es una problema en este comunidad? (Si o No)

10. En los ultimos 10 años, este problema….
    (ha incrementado)
    (esta igual)
    (ha disminuido)
    (NO SE)

CACERIA

11. Hay cacería dentro de la comunidad y en los bosques alrededores (en este area)? (Si o No)

Comentos:____
____

12. (Si) Ha notado cambios en la cantidad cacería en los últimos 10 años?
    (ha incrementado)
    (esta igual)
    (ha disminuido)
    (NO SE)

13. (Si) Cuantas personas de este comunidad?
    (mas o menos) están cazando?
    (Entre 1-5)
    (Entre 5-10)
    (Entre 10-15)
    (Mas que 15)
    (no se)

14. (Si) Lo cazadores son de la comunidad o de afuera?
(misma comunidad)
(otro comunidad)
(NO SE)

Cuales otros comunidades?
____
____
En que comunidad cazan mas?____________________

15. (Si) Porque razón están cazando?
(Económicas/para vender) __________________________
(Subsistencia/para comer) _________________________
(Deportivas/para divertir) _________________________
Otro____

16. (Si) Donde caza la mayoría de la gente?
(en sus fincas)
(en fincas de conocidos)
(en los parques)
(en reservas indígenas)
(donde sea)
(NO SE)

*usar mapa par poner lugares y áreas
donde la gente cazan

17. (Si) Cuantos <u>veces por mes</u> comen carne de monte en su casa?
(menos que 5)
(entre 5 y 10)
(entre 10 y 15)
(mas que 15)
(NO SE)

18. (Si) Cual es su carne favorita?_____________________

19. (Si) Otras que les gusta comer?______________________
____
____

20. (Si) Desde donde consigue esta carne? (caza) (compra)

<u>AREAS PROTEGIDAS</u>

21. Hay áreas protegidas (Parques Nacionales, Refugios de Vida Silvestre y Reservas Biológicas) cerca de aquí (de MINAE)?
(Si o No)

22. (Si)Cuales?____
____

23. (Si) Cree usted que estas áreas - *ayudan a la protección de los animales*?
(Si o No)
Porque?____

24. (Si) *Son suficientes para la protección de los animales*? (Si o No)
Porque?____

25. (Si) *Tienen algún beneficio para la gente local*? (Si o No)
Cuales?____

Con cual otro personal en este comunidad recomienda que hablemos sobre estos temas?_____________________________________

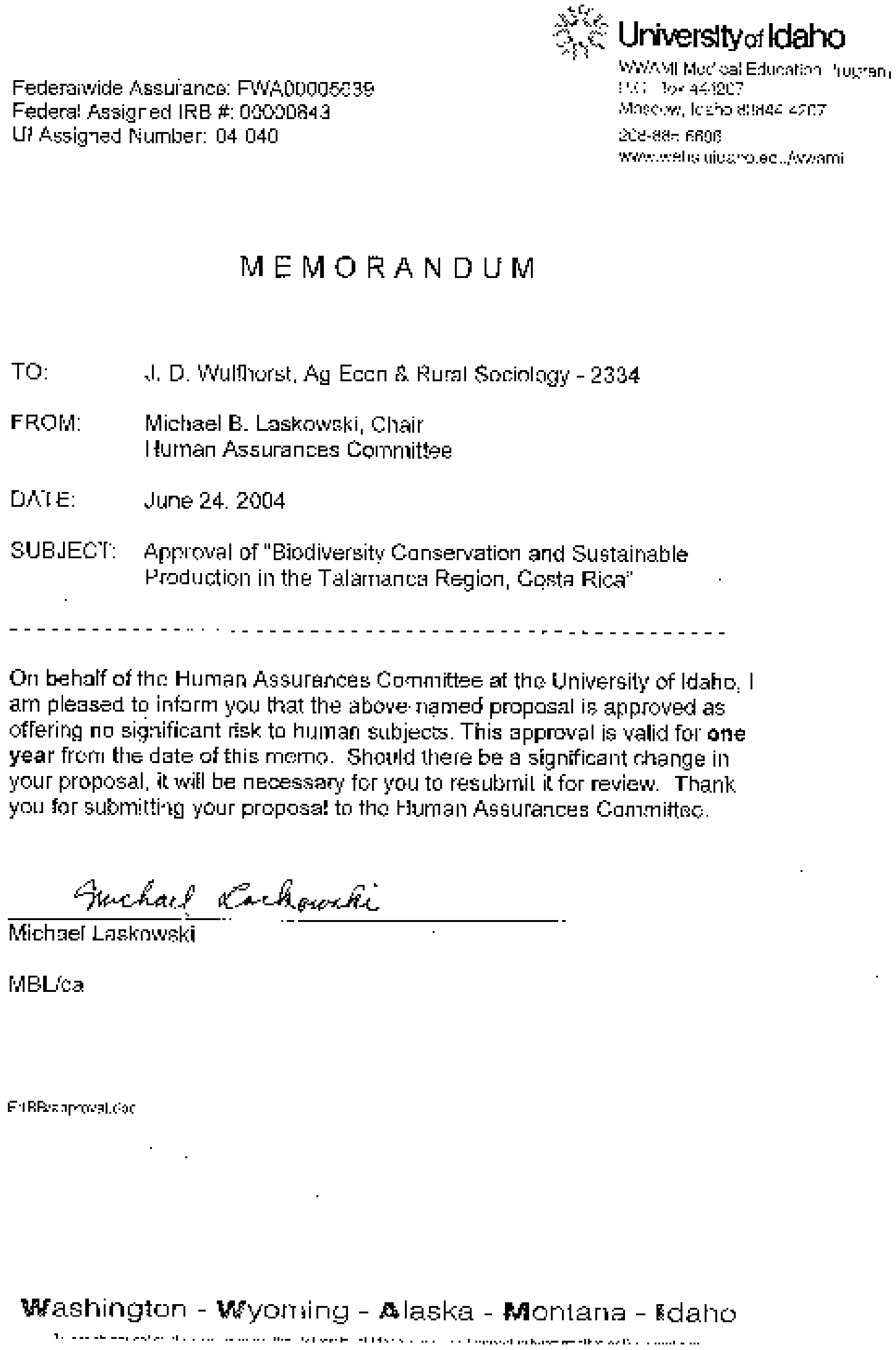
Si ellos NO SABEN no pone nada en la caja, si hay OTRA RESPUESTA que no es una opción (abajo) escríbala en la caja

Especias	Ultima vez que ha visto (cuando?)	Se cazan?	Porque razón cazan?	Observaciones
Jaguar				
Puma				
Chancho de monte				
Saino				
Tepezcuintle				
Danta				
Venado cola blanca				
Cabro de monte				
Guatuza				
Mono araña (colorado)				
Mono congo				
	(1 a 5 años) (6 a 10 años) (11 a 15 años) (16 a 20 años) (mas que 20 años)	(6 a 10 años) (11 a 15 años) (16 a 20 años) (mas que 20 años)	(e)conómico (vender) (s)ubsistencia (comer) (d)eportiva (divertir)	

Appendix B. Summary of species captured during the study. N(t)=total number of photos of species at all locations, M(c)= mean number of photos of species per location, TS=trap success (n/total TN x 100), Max cap=maximum # of captures per camera trap location, Loc. Cap.=number of camera trap locations captured, E=Evenness, D'= Simpsons diversity index, * denotes bird species

Family	Scientific name	Common name	IUCN 2009	N(t)	M(c)	TS	Max Cap.	Loc. Cap.	E	D`
Didelphimorphia	*Didelphis marsupialis*	Black-eared Opossum	LC	93	1.13	2.60	14	31	0.91	0.94
Didelphimorphia	*Philander opossum*	Gray Four-eyed Opossum	LC	8	0.10	0.22	5	3	0.82	0.53
Pilosa	*Tamandua mexicana*	Northern Tamandua	LC	17	0.21	0.47	5	12	0.92	0.87
Cingulata	*Dasypus novemcinctus*	Nine-banded Armadillo	LC	106	1.29	2.96	10	40	0.93	0.96
Primates	*Alouatta palliata*	Mantled Howler Monkey	LC	1	0.01	0.03	1	1	0	0.00
Primates	*Cebus capucinus*	White-throated Capuchin	LC	4	0.05	0.11	2	3	0.95	0.63
Rodentia	*Cuniculus paca*	Spotted Paca	LC	24	0.29	0.67	6	15	0.92	0.89
Rodentia	*Dasyprocta punctata*	Central American Agouti	LC	482	5.88	13.46	30	63	0.9	0.97
Rodentia	*Heteromys desmarestianus*	Demarest's Spiny Pocket Mouse	LC	14	0.17	0.39	5	6	0.88	0.76
Rodentia	*Proechimys semispinosus*	Tome's Spiny Rat	LC	13	0.16	0.36	5	5	0.89	0.73
Rodentia	*Sciurus granatensis*	Red-tailed Squirrel	LC	13	0.16	0.36	2	10	0.98	0.89
Carnivora	*Leopardus pardalis*	Ocleot	LC	33	0.40	0.92	8	16	0.88	0.88
Carnivora	*Leopardus wiedii*	Margay	NT	30	0.37	0.84	3	19	0.96	0.93
Carnivora	*Panthera onca*	Jaguar	NT	2	0.02	0.06	1	2	1	0.50
Carnivora	*Puma concolor*	Puma	LC	10	0.12	0.28	4	4	0.92	0.70
Carnivora	*Puma yagouaroundi*	Jaguarundi	LC	4	0.05	0.11	1	4	1	0.75
Carnivora	*Conepatus semistriatus*	Striped Hog-nosed Skunk	LC	29	0.35	0.81	7	16	0.91	0.89
Carnivora	*Eira barbara*	Tayra	LC	22	0.27	0.61	4	12	0.94	0.89
Carnivora	*Galictis vittata*	Greater Grison	LC	1	0.01	0.03	1	1	0	0.00
Carnivora	*Nasua narica*	White-nosed Coati	LC	165	2.01	4.61	19	41	0.9	0.95
Carnivora	*Procyon lotor*	Northern Raccoon	LC	86	1.05	2.40	15	24	0.91	0.93
Cetartiodactyla	*Mazama temama*	Central American Red Brocket	DD	1	0.01	0.03	1	1	0	0.00
Cetartiodactyla	*Pecari tajacu*	Collared Peccary	LC	37	0.45	1.03	10	11	0.91	0.86
Tinamiformes*	*Tinamus major*	Great Tinamou	LC	18	0.22	0.50	5	10	0.89	0.84
Galliformes*	*Crax rubra*	Great Curassow	NT	53	0.65	1.48	11	20	0.86	0.89
Gruiformes*	*Aramides cajanea*	Rufous-necked Wood-Rail	LC	13	0.16	0.36	6	4	0.87	0.66
Columbiformes*	*Leptotila cassini*	Gray-chested Dove	LC	36	0.44	1.01	25	9	0.56	0.50

Appendix C University of Idaho Human Subjects Study Approval



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Federalwide Assurance: FWA00005639
Federal Assigned IRB #: 00000843
UI Assigned Number: 04 040

MEMORANDUM

TO: J. D. Wulfhorst, Ag Econ & Rural Sociology - 2334

FROM: Michael B. Laskowski, Chair
Human Assurances Committee

DATE: June 24, 2004

SUBJECT: Approval of "Biodiversity Conservation and Sustainable Production in the Talamanca Region, Costa Rica"

On behalf of the Human Assurances Committee at the University of Idaho, I am pleased to inform you that the above-named proposal is approved as offering no significant risk to human subjects. This approval is valid for **one year** from the date of this memo. Should there be a significant change in your proposal, it will be necessary for you to resubmit it for review. Thank you for submitting your proposal to the Human Assurances Committee.

Michael Laskowski

Michael Laskowski

MBL/ca

F:\IRB\approval.doc

Washington - Wyoming - Alaska - Montana - Idaho

Chapter Four

Comprehensive conservation planning: developing a framework for planning across terrestrial, freshwater and marine ecosystems**

Abstract

Systematic conservation planning methods are widely used to identify conservation priority areas, and for a variety of reasons have traditionally considered terrestrial, freshwater, and marine ecosystems separately. Many physical and ecological processes link these ecosystems, however, affecting biodiversity in all three realms. These interactions suggest that an integrated planning approach could more effectively conserve biodiversity. Comprehensive conservation planning for terrestrial and aquatic ecosystems poses significant challenges, and a critical evaluation of available methods is currently lacking. Here we discuss the goals of comprehensive conservation planning in general and in the specific context of a planning domain on the Caribbean slope of Costa Rica and Panama, and then review strategies currently being used to develop conservation plans for multiple realms. All of the methods we review can be used to improve integration of planning efforts for terrestrial and aquatic systems, but there is a trade-off between ease of application and the consideration of ecological linkages among realms in the planning process. Although several of the methods we review would be applicable to comprehensive planning in our study site, models needed to incorporate biophysical interactions among realms into conservation planning algorithms remain poorly developed. Given the limited capacity for expanding protected area networks in most regions, and the way that matrix lands affect existing protected areas in multiple realms, there is a great need to develop new comprehensive planning tools that can direct a broader array of conservation interventions.

Introduction

The loss of biodiversity is among the greatest challenges currently facing humanity (Pimm et al 1995, Dirzo and Raven 2003). Species and even entire ecosystems are going extinct at a rate far greater than ever before, in what has been referred to as the 6th extinction crisis (Pimm and Brooks 2000). The biodiversity crisis appears to be particularly severe in freshwater ecosystems

(Abell 2002, Malmqvist and Rundle 2002), where rates of extinction and endangerment may be even higher than in terrestrial environments (Ricciardi and Rasmussen 1999, Revenga et al. 2005).

In response, there has been increased attention given to gaps in the current global protected areas network (Rodrigues et al. 2004a), as well as calls for improving conservation on private lands outside of reserves (O'Connell and Noss 1992, Knight 1999). There is continued debate about how much of the planet should be protected (Brooks 2004, Tear et al. 2004), and whether efforts should focus on species (Brooks et al. 2004), ecosystems (Higgins et al. 2004), or ecosystem function (Moss 2000). Nevertheless, the establishment of a representative network of protected areas which covers all biomes and species is a widely recognized target scientifically (Brooks 2004, Rodrigues et al. 2004a, Rodrigues et al. 2004b) and politically (Convention on Biological Diversity 1992).

Systematic conservation planning methods have been developed during the last 20 years in response to the need to move beyond ad-hoc reserve selection and to set measurable targets, strategies and goals for the design of protected areas (Margules and Pressey 2000). These methods are used to identify potential reserve networks that represent the full range of species and ecosystems in a given planning area and are spatially efficient, recognizing the scarcity of resources available for conservation and the need to balance conservation goals with other societal values (Sarkar et al. 2006). Systematic conservation planning methods are now widely used to identify conservation priority areas in both terrestrial and marine systems. Applications in freshwater environments are less common (Sarkar et al. 2006), but several recent examples illustrate how these methods can be adapted to freshwater planning (Abellán et al. 2005, Linke et al. 2007).

For a variety of institutional and logistical reasons, systematic conservation planning for terrestrial, freshwater, and marine realms has usually been conducted separately (Beger et al. In Press). Conservation planning is an inherently complex process and even in the most thoroughly studied areas in the world there is high uncertainty concerning the distribution of biodiversity (Margules et al. 2002) and threats to its persistence (Gaston et al. 2002). For aquatic ecosystems, even the most basic information needed to assess conservation priorities may be scarce (Abell 2002). Planning in different realms requires expertise in different fields of research, and entirely different governmental agencies or non-governmental organizations are often involved in management and conservation of the different ecosystems (Beger et al. In Press). Biogeographical patterns, ecological processes, and the relative importance of different threats to biodiversity also differ among terrestrial, freshwater, and marine ecosystems. As a result, conservation planning in different realms may involve very different considerations (Carr et al. 2003 Dunn 2003, Abell et al. 2007) and methods (Higgins et al. 2005). Together these factors constitute a considerable barrier to development of comprehensive planning approaches for terrestrial and aquatic ecosystems.

Despite these challenges, there is a growing recognition of the limitations of a fragmented approach to conservation planning (Beger et al. In Press). Freshwater, marine, and terrestrial ecosystems are strongly linked by fluxes of water, sediment, nutrients and organisms (e.g. Hynes 1975, Polis et al. 1997, Nakano and Murakami 2001, McDowall 1998), which have a critical influence on biodiversity in all three realms. The relevance of these interactions to conservation is particularly conspicuous for aquatic ecosystems, where many of the most important threats to biodiversity are directly linked to activities in terrestrial landscapes upslope and upstream (Allan 2004, Thrush et al. 2004, Stoms et al. 2005, Burcher et al. 2007). Resource fluxes from aquatic ecosystems can have significant effects on productivity and community composition in terrestrial environments, as well (Nakano and Murakami 2001, Polis et al. 2004, Crait et al. 2007). These interactions are particularly important in transition zones like riparian areas, which also support unique communities (Sabo et al. 2005). Given this interdependence among ecosystems, comprehensive planning approaches that consider functional interactions between terrestrial and aquatic environments are likely to produce more robust conservation assessments (Stoms et al. 2005, Beger et al., In Press).

Recognition of the potential advantages of conducting comprehensive conservation assessments has led to an increasing number of conservation plans that identify priority areas for terrestrial and aquatic biodiversity in a common planning domain. A variety of methods have been used to develop these plans, representing varying levels of integration in the planning process. However, it remains unclear how effectively these methods incorporate interactions among realms, the primary impetus for a comprehensive approach. In addition, different methods may be appropriate in different situations, depending on the availability of data and expertise, the nature of terrestrial-aquatic interactions in the planning area, and the specific goals of the conservation assessment. Unfortunately, there is currently very little information to guide decisions on planning methodology. A critical evaluation of the methods currently being used to integrate terrestrial and aquatic conservation goals could help direct efforts by conservation practitioners and suggest directions for future research.

In this paper, we begin by discussing the goals of comprehensive conservation planning, using a planning domain on the Caribbean slope of Central America as an example. Next, we summarize the strategies that have been used, or proposed, to produce conservation plans that include terrestrial and aquatic ecosystems. Each strategy is then evaluated based on several criteria, including data requirements, methodological difficulty, and the degree to which functional interactions between ecosystems are represented. Based on this evaluation, we present a set of methods that would be most useful for comprehensive planning in our example planning domain, and discuss future developments in conservation planning. Throughout our discussion, we use the term conservation planning to refer to the process of identifying potential reserve networks using systematic reserve selection algorithms and spatial decision support software, although reserve selection is just one part of the conservation planning process (Knight et al. 2006).

Goals of a comprehensive planning approach

Systematic conservation planning aims to identify an array of sites that, if managed properly, could provide for the persistence of the full complement of biodiversity in a given region (Margules and Pressey 2000). In practice, this usually entails selecting a set of priority sites based on the distribution of a few relatively well-studied groups, as well as the occurrence of habitat types that can be identified through remote sensing or unique combinations of biophysical factors like soil, elevation, and precipitation (Margules et al. 2002, Higgins et al. 2005). The extent to which plants and vertebrates, which are most often used as surrogates for biodiversity patterns, represent broader patterns of biodiversity remains an important, and unanswered, question. The ability of habitat types (e.g. land cover types) to represent patterns of biodiversity has been established in some cases, but remains poorly understood in general

(Brooks et al. 2004). Despite these problems, the use of biodiversity surrogate groups and habitat types in conservation planning is a pragmatic approach to incorporating the best available information into the planning process (Pressey 2004).

Planning for the persistence of all species and ecosystems, terrestrial and aquatic, in a given area is a logical extension of the systematic planning approach. Ideally, a comprehensive plan would meet several key goals. First, it would identify a network of sites where known biodiversity features in terrestrial and aquatic ecosystems, including individual species and entire communities, are fully represented. In addition, potential reserves would be extensive enough to maintain viable populations of all species and sustain ecological processes (e.g. disturbance regimes) necessary for the long-term persistence of all biodiversity features. These goals have typically been addressed in conservation planning through the size of potential reserves, identifying corridors among these sites, and steering reserve selection away from sites with heavy human impacts (e.g. Noss et al. 1999, Cowling et al. 2003, Mattson and Angermeier 2007). In a comprehensive approach, these factors would still be relevant, but two additional considerations would also be important. First, reserve selection methods should consider spatial relationships between sites in different realms that sustain key biophysical processes (Figure 1). For example, the spatial arrangement of coral reefs and mangroves could influence the abundance and persistence of species that use both ecosystems during their life cycle (Mumby 2006). Second, a comprehensive planning approach would ideally identify a network of conservation priority areas that minimizes threats to biodiversity in all realms, recognizing that threats can move between realms and follow directional flows in aquatic ecosystems.

An example planning domain

The goals of a comprehensive assessment can be illustrated using an example planning domain that includes terrestrial, freshwater and marine ecosystems. Our example is located on the Caribbean slope of Central America in southeastern Costa Rican and northwestern Panama. The terrestrial portion of the planning domain covers approximately 3800 km^2 and encompasses the Estrella and Sixoala River basins and the smaller coastal drainages between them (Figure 2). This area is located within the Mesoamerican biodiversity hotspot (Myers et al. 2000, Mittermeier et al. 2005), and includes portions of the Talamanca montane ecoregion, a Global

200 priority ecoregion (Palminteri et al. 1999, Olson and Dinerstein 2002). The flora and fauna of this area are extremely diverse due to the wide variety of life zones, and to the fact that is it a convergence zone for fauna from North and South America (Graham 1995). The area is also rich in endemic birds, mammals, herpetofauna and plants (Palminteri et al. 1999). The inland backbone of the Talamanca Mountains is drained by a network of rivers that support diverse vertebrate and invertebrate communities, including several freshwater fish species endemic to the region (Bussing 1998). Nearshore marine environments are also included in our planning domain and are exceedingly diverse, with some of the largest coral reefs in Costa Rica (Cortes 1998). Transition zones between ecosystems in this landscape include floodplain lakes and wetlands, riparian forests, estuaries, mangroves, lagoons, and beaches. These interfaces provide critical habitat and breeding grounds for many of the region's rare and threatened species, such as estuarine nurseries for the Atlantic tarpon or beach nesting sites for sea turtles (Wilkinson 2004, Cortez 1998).

Several protected areas, including La Amistad International Park, Chirripò National Park, Hitoy-Cerere Biological Reserve, Cahuita National Park, Gandoca-Manzanillo National Wildlife Refuge, and a number of smaller private reserves have already been established in the region (Boza 1986). The current system of protected areas is extensive (Figure 2), but highly skewed toward to high-elevation montane forests and coastal swamps, leaving many of the most diverse ecosystems in the region underrepresented (Palminteri et al. 1999, Powell et al. 2000). Cahuita National Park and Gandoca-Manzanillo National Wildlife Refuge protect terrestrial and marine environments, and nearly all of the coral reefs in the area. Land tenure outside of protected areas includes private lands owned by small landholders and large corporations, as well as several indigenous reserves that together occupy nearly 30% of the planning domain and form a buffer zone around montane protected areas. Common land uses in indigenous reserves include plantain production, banana and cacao agroforestry systems, and shifting cultivation of basic grains, while intensive monocultures of banana and plantain, cattle pasture, and tourism development predominate on private lands outside reserves. Banana and plantain production is concentrated in the floodplains of the Sixaola and Estrella River systems, where plantations receive year-round pesticide applications of up to 50 kg of active ingredient/ha/yr for export-quality fruit (B. Polidoro et al. 2008).

Principal threats to biodiversity in this region include logging (Palminteri et al. 1999), intensive agriculture and agrochemical use (Borge and Castillo 1997, Castillo et al. 2006), illegal hunting and fishing (J. Schipper, unpublished data), and siltation in nearshore marine environments (Cortes and Risk 1985). Coastal development also poses a potential risk to biodiversity in multiple ecosystems, but the severity of this risk is largely unknown. Although most floodplain environments in the area have been severely altered, the terrestrial portion of the planning domain is one of the most intact landscapes in the region. Freshwater and marine ecosystems in the planning domain are also significant on a national level, and so there is an urgent need for strategic conservation planning in the area to ensure the long-term persistence of terrestrial and aquatic biodiversity.

A comprehensive conservation plan for our planning domain would ideally include several key components. First, the plan would identify a suite of sites that could complement the existing reserve network and allow for the persistence of species and ecosystems that are not adequately protected in existing reserves. In practice, this would mean identifying an array of sites at low to mid-elevations that support species and communities that are poorly represented in current protected areas. Ideally, these sites would be selected based on their connectivity with existing protected areas, as well as their importance for seasonal migrations of organisms, dispersal and recruitment processes, and natural disturbance regimes within terrestrial, freshwater, and marine realms. Second, the plan would target transition zones between realms, including floodplains and estuaries, which are particularly important for biodiversity conservation. These habitats could be mapped and considered as unique habitat types to be included in representation goals. Third, an effective comprehensive plan would identify a set of priority sites that minimizes threats to biodiversity throughout the reserve network. This is a particularly important aspect, as existing reserves are threatened to varying degrees by exogenous factors (e.g. sediment deposition on reefs) that threaten to undermine conservation objectives. Finally, a comprehensive plan would ideally promote the maintenance of ecosystem services (Chan et al. 2006) and maximize economic benefits to local communities (Naidoo and Ricketts 2006).

Methods for integrated conservation planning

A review of the conservation literature yielded a variety of conservation plans that use terrestrial and aquatic biodiversity features to identify a set of conservation priority areas (Table 1). These plans used diverse approaches to identify priorities, ranging from heavy dependence on expert opinion to systematic approaches driven by selection algorithms and spatial decision support systems. Methods for targeting terrestrial and aquatic biodiversity features also differed greatly among the plans we reviewed. The examples we present are not an exhaustive list, but were selected to illustrate the range of approaches that have been used. Most of these examples focus on terrestrial and freshwater ecosystems, but several recent conservation plans have also included marine conservation goals (Table 1). Based on our review of these plans and other relevant literature, we identified seven methods for developing comprehensive conservation plans for terrestrial and aquatic realms (Table 2). These approaches vary from post-hoc comparisons of conservation priorities based on independent assessments of freshwater, terrestrial, and/or marine environments in a particular geographic area to increasingly integrated approaches. Below, we evaluate each of these methods based on planning efficiency, ease of application using existing software, data requirements compared with planning for each realm separately, and the extent to which interactions between realms are considered when selected priority areas (see Table 2).

Method 1. Develop separate conservation plans for terrestrial, freshwater, and/or marine realms and then overlay results.

This is the simplest approach methodologically, and in terms of data requirements. Once separate conservation plans for terrestrial and aquatic realms have been developed, priority areas can easily be overlaid in a geographic information system. This method is particularly well-suited to integration across freshwater and terrestrial realms because of the way that freshwater ecosystems are embedded in terrestrial landscapes. Simple overlays in this case may provide considerable insight into synergies or trade-offs between freshwater and terrestrial conservation priorities. Marine systems are more spatially distinct, but overlays may still be informative for coastal areas and islands, where protected areas could include multiple realms.

Maintaining separate planning processes for terrestrial and aquatic ecosystems may allow for more thorough and relevant assessments of biodiversity priorities in each realm, and does not require that similar data are available for both. However, the effort required to develop completely separate plans makes this a relatively inefficient approach, especially if similar data and software are being used in the planning process. In some areas, conservation assessments for one or more realms already exist, and utilizing this information in an overlay approach could significantly reduce the cost of producing a comprehensive plan. Linkages between realms are very poorly represented with this approach, although assigning higher priority to areas of spatial congruence between realms may capture sites where functional relationships are intact. Using expert opinion to modify priority areas based on overlays can also improve integration across realms.

Method 2. Target terrestrial and aquatic habitat types when selecting conservation priority areas: a coarse-filter approach.

As discussed above, targeting habitat types for protection in conservation planning is a pragmatic approach to deal with uncertainty concerning the distribution of most species. Habitat types (also referred to as land types or ecological systems) are often called coarse-filter targets because they are thought to capture large and poorly known complements of species (Groves et al. 2002). Planning using terrestrial and aquatic habitat types as coarse-filter targets is straightforward methodologically, and is an efficient way to incorporate data from both ecosystems in a single analysis. Furthermore, this approach gives equal weight to terrestrial and aquatic biodiversity through representation of all habitats in the planning domain.

Data requirements for this method may be higher than for conducting separate assessments, primarily because of the need for comparable data across realms. Maps of terrestrial habitats are often readily available or can be produced using remote sensing and other spatial data. Similar methods typically cannot be applied to aquatic systems, and so producing accurate maps of marine and freshwater habitats can be more difficult. Significant progress has recently been made in this area for freshwater systems (Higgins et al. 2005, Thieme et al. 2007), offering new opportunities for integration across realms. Other issues of scale are also relevant, especially in practice. First, the different shapes and spatial extents of ecological systems in different realms can make display very difficult, especially when spatial decision support systems are being used to explore conservation trade-offs. Boundaries between realms are particularly complicated, as they are often temporally dynamic (e.g. floodplains, tidal marshes) and difficult to delineate. Explicitly targeting transition zones for protection could alleviate many of these problems, ensuring that features in both realms, and the ecological processes they support, are adequately represented (Beger et al. In Press). Aside from capturing transition areas, this method does not effectively address linkages among realms.

Method 3. Target terrestrial and aquatic species when selecting conservation priority areas: a fine filter approach.

Although targeting specific habitat types for conservation may capture most species and assemblages, these areas may not provide adequate protection for species that depend on very specific habitats, have limited ranges, or require extraordinarily large areas to maintain viable populations. Targeting these species of special conservation concern provides a fine filter that complements the coarse-filter approach (Groves et al. 2002). The geographic distribution of focal species can be represented spatially as point occurrences or as polygons based on known areas of occupancy, habitat suitability models or expert opinion. The quality of species occurrence data varies widely, and is often heavily biased even in the best-studied areas (Margules et al. 2002, Pressey 2004). Nevertheless, once data have been standardized to a common format, fine-filter targets from different ecosystems can be treated equally in the planning process. Using fine-filter targets from terrestrial and aquatic ecosystems in this way can improve the efficiency of the planning process while using existing data and planning methods.

Like the coarse-filter approach discussed above, using fine-filter targets from terrestrial and aquatic ecosystems does little to address linkages among realms and their influence on biodiversity. Selecting focal species like amphibians, otters, or wading birds that rely on habitats in more than one realm could help, because their ranges may capture transition zones between realms. However, even for these species, there is no guarantee that key spatial relationships between habitats in different realms will be captured with this approach.

Method 4. Use conservation assessment for one realm as a “seed” for identifying priorities in other realms.

When a conservation assessment has already been made for one realm, the selected priority areas can be used to guide reserve selection in other realms. This method has been used to select potential marine reserves based on their spatial congruence with previously selected terrestrial priority areas (e.g. Floberg et al. 2004), and to modify an existing terrestrial conservation assessment so that it better represents freshwater biodiversity features (Abell et al. 2004). This approach is relatively efficient where a systematic conservation assessment for one realm has already been developed, and has minimal extra data requirements compared with planning for a single realm. Using one assessment as a starting point for others is quite similar to locking in existing protected areas when conducting a systematic conservation assessment (e.g. Cowling et al. 2003), and can be accomplished using available software tools. The extent to which ecosystem linkages are represented with this approach depends on how additional conservation priority areas are selected. For example, if spatial congruence with an existing set of sites is emphasized using a boundary length function in the selection algorithm, important functional linkages among ecosystems may be preserved incidentally. Nevertheless, because the initial set of priority areas are locked in without considering linkages with other realms, sites that are most important for maintaining these linkages and minimizing threats to biodiversity may be overlooked.

Method 5. Automatically select transition areas adjacent to aquatic conservation priority areas (e.g. floodplains).

As noted above, ecological processes that operate in transition zones where two realms meet are often vital to maintaining biodiversity in both realms. One alternative for representing these functional relationships in a comprehensive planning approach is to include parts of adjacent ecosystems when selecting priority areas. For example, riparian areas adjacent to streams targeted for protection could automatically be included as priority areas for conservation action. Shorelines adjacent to marine protected areas could also be targeted. This strategy is relatively straightforward to apply and, similar to the explicit mapping of transition zones, may protect unique biological communities and ecological processes that occur in transition zones.

Deciding exactly how much area to protect in the adjacent ecosystem is not as straightforward, and additional spatial data on the occurrence of certain vegetation types or other indicator species may be needed to determine appropriate dimensions for transition areas. Digital elevation models can be used to map geomorphic surfaces and provide information on the spatial extent of floodplains and other transition zones, even in data-poor regions (Thieme et al. 2007). Despite the advantages of this method, aquatic ecosystems are affected by land use and other impacts in their catchments at multiple spatial scales (Allan 2004), and so protecting narrow transition zones alone may not be sufficient to maintain important functional linkages among ecosystems.

Method 6. Use river basin boundaries to define the planning domain and small catchments as planning units

Freshwater ecosystems are strongly linked to the surrounding landscape, and so freshwater protected areas function best when reserves protect entire catchments (Crivelli 2002, Saunders et al. 2002, Abell et al. 2007). Using catchments as planning units, therefore, is an efficient approach to identifying priority areas that are relevant to terrestrial and aquatic conservation goals. Applying this approach is relatively simple, as watersheds can be mapped at multiple spatial scales using digital elevation models to match the target size for planning units. In addition, catchments are naturally nested in a way that facilitates spatial aggregation of planning units into larger reserves. Upstream-downstream connectivity rules can also be used to ensure that priority sub-catchments are not selected downstream from unprotected areas (Linke et al. 2007). Nearshore marine environments are similarly affected by landscapes “upstream” (Stoms et al. 2005), and could benefit from conservation at the catchment scale.

The major drawback to using catchments as the basis for comprehensive conservation planning is the mismatch between terrestrial and freshwater planning domains. Terrestrial ecoregions, the most common planning domain for terrestrial assessments, are rarely congruent with the catchment boundaries that define freshwater biogeographic units (Abell et al. 2002). This creates non-trivial issues of scale for comprehensive assessments, as representation and complementarity criteria depend on how much of a river basin or terrestrial ecoregion is included in the planning domain (e.g. Floberg et al. 2004). This issue is a fundamental challenge that cuts across many of the methods reviewed here, and can only be circumvented by developing separate conservation plans for freshwater and terrestrial ecosystems.

Method 7. Explicitly consider ecological linkages between realms in reserve selection algorithms.

Conservation planning tools that incorporate biophysical interactions between terrestrial and aquatic ecosystems have the potential to produce more realistic conservation assessments and allow for more robust evaluations of the benefits of specific conservation actions (Stoms et al. 2005, Beger et al. In Press). These interactions could include natural processes that contribute to the development and maintenance of biodiversity (e.g. diadromous fish migration, allochthonous resource subsidies among realms), as well as processes that threaten biodiversity (e.g. transport of sediment and pollutants between realms). Beger et al. (In Press) provide a thorough review of these topics, as well as specific methods for targeting a variety of ecological interactions between realms in systematic conservation assessments.

The main limitation of this approach is the difficulty of accurately describing and predicting ecosystem interactions across realms (Stoms et al. 2005). Many of the most important processes can be described qualitatively, but precise quantitative descriptions are much more difficult to develop. In some cases, such detail may not be crucial and relatively simple heuristic rules can be used. This approach has often been used to steer reserve selection away from areas with high human impact, using variables like road density. Accurate, spatially-explicit models describing movement of organisms, water, sediment, nutrients, and contaminants among realms would clearly be superior to qualitative approaches. However, data needed to parameterize these models is often limited or completely absent, particularly in developing regions. Spatial and temporal variation in these processes further complicates modeling and prediction. Finally, even if there was sufficient information to accurately predict how land-use change will affect key biophysical processes operating among realms, linking these models to decision support systems to examine trade-offs among individual sites presents another level of complexity.

Discussion: application to the example planning domain

The conservation planning methods reviewed above are not mutually exclusive, and several may be appropriate when developing a comprehensive conservation plan. Here we discuss the applicability and feasibility of each method for our example planning domain. We are not aware of any systematic planning efforts in the study region that have been conducted at a scale relevant to our planning domain, and so building on an existing plan (Method 4) is not an option in this area. The lack of previous planning efforts and high connectivity among ecosystems suggests that conducting separate conservation assessments for terrestrial, freshwater and marine environments (Method 1) would also be an inefficient and ineffective method.

Among the remaining methods, targeting specific habitats and species (Methods 2 and 3) would both be feasible in our study area. Maps of terrestrial habitat types (Kappelle et al. 2002) and nearshore marine ecosystems are available for the planning domain, and freshwater habitats could be mapped using available digital elevation data. In addition, the most important transitional ecosystems could be mapped using existing digital elevation data, aerial photos, and satellite imagery. Occurrence data within the planning domain exist for many terrestrial and aquatic species of conservation concern, including birds and amphibians (www.natureserve.org), mammals (Harvey et al. 2006, J. Schipper, unpublished data), freshwater fishes (Bussing 1998, C. Lorion, unpublished data), and reef-building corals (Cortes 1998). Available occurrence data may not necessarily represent viable populations because most data are from short-term surveys rather than demographic studies. Nevertheless, targeting known biodiversity features in all realms would be an essential component of a comprehensive planning approach, and priority areas could be updated as new data became available. Boundary length constraints could also be used during reserve selection to improve connectivity within the reserve network, which could increase the long-term viability of small, fragmented populations and species with large area requirements.

Targeting specific species and ecosystems would not adequately address linkages between ecosystems and their influence on biodiversity, and so other methods would also be needed to produce an effective comprehensive plan. Including transition areas adjacent to freshwater and marine protected areas (Method 5) could help maintain functional relationships among realms, but may be redundant if transition zones are targeted directly. Furthermore, transition areas may already be protected by law (e.g. Costa Rican law prohibits clearing streamside forests). The limitations of protecting transition zones are evident in Cahuita National Park, where terrestrial and freshwater systems immediately adjacent to the marine environment are protected, but reef systems continue to be affected by sediment and contaminants from outside the protected area (Cortes and Risk 1985, Cortes 1998).

Using a catchment-based approach to define conservation priority areas (Method 6) is most likely to reduce threats to aquatic ecosystems, and explains why we defined our study area by watersheds as opposed to political boundaries. Small sub-catchments 10-20 km^2 in size could be mapped as planning units for our study area using readily available digital elevation data. The major problem with this approach is the lack of spatial congruence between terrestrial ecoregions and watershed boundaries in the study region. All major river basins in the region are divided by terrestrial ecoregion boundaries, with higher elevation areas on both slopes of the Talamanca Mountains located within the Talamanca montane ecoregion, and lower elevation areas defined by different terrestrial ecoregions (Palminteri et al.1999). This arrangement makes it difficult to assess how terrestrial conservation priority areas fit into ecoregional-scale representation of species and ecosystems, but cannot be avoided if catchments are used as the basis for planning.

Finally, effective conservation in our planning domain will require the maintenance of key ecosystem processes operating between terrestrial, freshwater, and marine ecosystems, as well as mitigation of threats that move among these realms. Specifically targeting ecological processes for protection using reserve selection algorithms (Method 7) could be done in several ways. First, as mentioned above, transition areas like riparian zones and shorelines could be mapped as distinct features and linked to protected areas in adjacent realms using boundary length constraints. Longer connections among reserves, such as migratory pathways for diadromous fishes, could also be identified and targeted using available reserve selection algorithms (Beger et al. In Press). Concerning threats, simple heuristic rules could be used to prioritize potential terrestrial reserves based on their potential to affect aquatic ecosystems downstream either positively or negatively (Stoms et al. 2005).

Integrating reserve selection algorithms with process models describing the flow of water, nutrients, sediment, and contaminants could provide a much clearer picture of trade-offs between different potential reserves. However, data to parameterize these models are generally lacking for the study region. Even though sedimentation and contamination are known to threaten numerous aquatic species and ecosystems in Costa Rica and other tropical coastal landscapes (Castillo et al. 2006, Wishnie and Socha 2003, Peters et al. 1997, Cortes and Risk 1985), their rates are difficult to predict and often exhibit high natural variability (Krishnaswamy et al. 2001).

Conclusions

A comprehensive approach to conservation planning that identifies priority areas based on biodiversity patterns in terrestrial and aquatic ecosystems, as well as biophysical interactions between these realms, has great potential to produce more effective reserve networks. However, realizing this potential will require the development of new tools for assessing exactly how reserve selection will affect biodiversity in all realms. Such tools could also be used to inform decisions about a broader array of conservation interventions, including habitat restoration and application of best management practices on private lands. These interventions would be particularly important in heavily modified landscapes where conservation opportunities are limited. Even in a relatively intact landscape like our example planning domain, the capacity for setting aside more protected areas is severely limited by land tenure and land use patterns and the resources available for conservation. Furthermore, setting aside more protected areas in this landscape may do less to ameliorate threats to aquatic biodiversity than improving land management practices and simply enforcing current laws.

There is good evidence that agricultural land uses in this domain vary greatly in their capacity to support native biodiversity (Harvey et al. 2006, Harvey and Gonzalez 2007), but the effects of different land uses on biodiversity in freshwater and marine ecosystems remain very poorly understood. Incorporating trade-offs between reserve designation, land-use practices, and biophysical processes into a comprehensive planning framework may seem hopelessly complex, but it may be the only way to find conservation solutions that best serve society. Private lands will always contribute at some level to conservation, and when these values are not included in the planning process, optimal solutions to complex planning problems may be missed (Faith and Walker 2002, Polasky et al. 2005).

The need to look beyond strict reserves in comprehensive planning approaches is particularly clear when considering freshwater conservation goals. Although strict protection of entire catchments is the ideal approach for freshwater biodiversity conservation, this strategy is infeasible for most river systems. Thus, effective conservation of freshwater biodiversity will require a broader perspective on protected areas that includes areas specifically managed to meet conservation goals while providing other economic opportunities (Abell et al. 2007). Expanding terrestrial reserve networks may help to achieve this goal, but eliminating destructive land uses is just as important. Ecological risk assessment provides a ready framework for identifying sites that pose the greatest threat to biodiversity, and incorporating these methods into the planning process could significantly advance comprehensive assessments. The challenge is to link these models with conservation planning algorithms in decision support systems to explore trade-offs and search for optimal solutions. Conservation planning has a long way to go to achieve these goals, but development of comprehensive planning techniques based on a broader perspective of conservation action may significantly improve our ability to conserve biodiversity in all realms.

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Table 1. Examples of conservation assessments that include targets and/or identify priority areas for terrestrial and aquatic ecosystems, arranged in chronological order.

	Author	**Geographic Area**	**Terrestrial**	**Freshwater**	**Marine**	**Software**
1	Noss et al. 1999	Klamath-Siskiyou Ecoregion, USA	x	x		None a
2	TNC 2000	Middle Rockies-Blue Mountains Ecoregion, USA	x	x		SITES
3	TNC 2001	North Coast California Ecoregion, USA	x	x		None a
4	Noss et al. 2002	Greater Yellowstone Ecosystem, USA	x	x		SITES
5	TNC 2002	Chesapeake Bay Lowlands Ecoregion, USA	x	x	x	None b
6	Cowling et al. 2003	Cape Floristic Province, South Africa	x	x		C-PLAN
8	TNC 2003a	Cook Inlet Basin Ecoregion, USA	x	x	x	SITES
7	TNC 2003a	West Gulf Coastal Plain Ecoregion, USA	x	x		None b
9	Weitzell et al. 2003	Upper Mississippi River Basin, USA	x	x		None b
10	Floberg et al. 2004	Willamette Valley-Puget Trough- Georgia Basin Ecoregion, North America	x	x	x	SITES
11	Marshall et al. 2004	Apache Highlands Ecoregion, USA	x	x		SITES
12	TNC 2004	Federated States of Micronesia	x	x	x	None b
13	WWF 2006	Guinean-Congolian Region, Africa	x	x		None b
14	Huggins et al. 2007	Insular Caribbean	x	x	x	MARXAN
15	Schoen and Albert 2007	Southeast Alaska, USA	x	x		MARXAN

[a] priority areas selected based on number of targets and suitability criteria

[b] conservation portfolio designed based on expert opinion

Table 2. Methods for developing comprehensive conservation plans across terrestrial and aquatic ecosystems, with references that discuss or apply each approach.

Planning Method	**References**	**Planning Efficiency**	**Technical Difficulty**	**Data Requirements**	**Ecosystem Linkages**
1. Develop separate conservation plans for terrestrial and aquatic ecosystems and then overlay results	TNC 2002, Weitzell et al. 2003, TNC 2003b	Low	Low	Low	Low
2. Target terrestrial and aquatic habitat types when selecting conservation priority areas	TNC 2000, TNC 2001, Noss et al. 2002, TNC 2003a, Huggins et al. 2007	Moderate	Low	Moderate	Low
3. Target terrestrial and aquatic species when selecting conservation priority areas	TNC 2000, TNC 2001, Noss et al. 2002, Cowling et al. 2003, TNC 2003a	Moderate	Low	Low	Low
4. Use conservation assessment for one realm as a "seed" for identifying priorities in other realms	Abell et al. 2004, Floberg et al. 2004	Moderate	Low	Low	Moderate
5. Automatically select transition areas adjacent to aquatic conservation priority areas (e.g. floodplains)	TNC 2003b	Moderate	Low	Low	Moderate
6. Use river basin boundaries to define planning domain	TNC 2000, TNC 2001	High	Low	Low	Moderate

Figure 1. Examples of biotic and abiotic linkages among terrestrial, freshwater, and marine ecosystems.

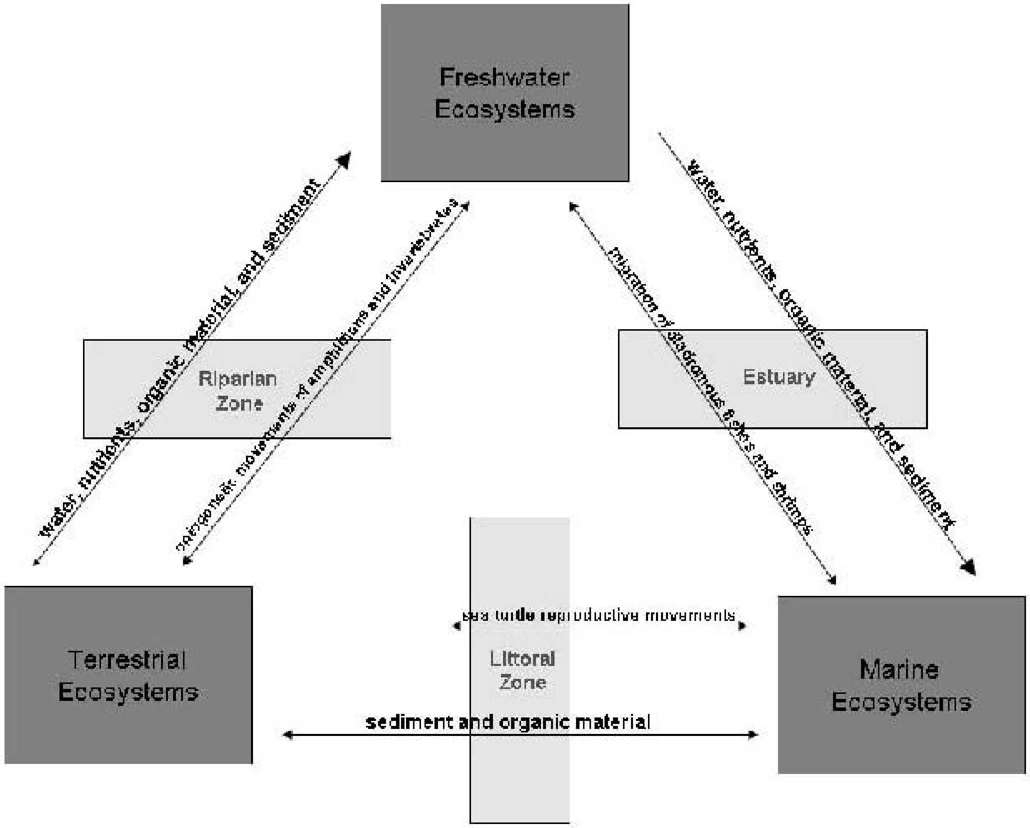
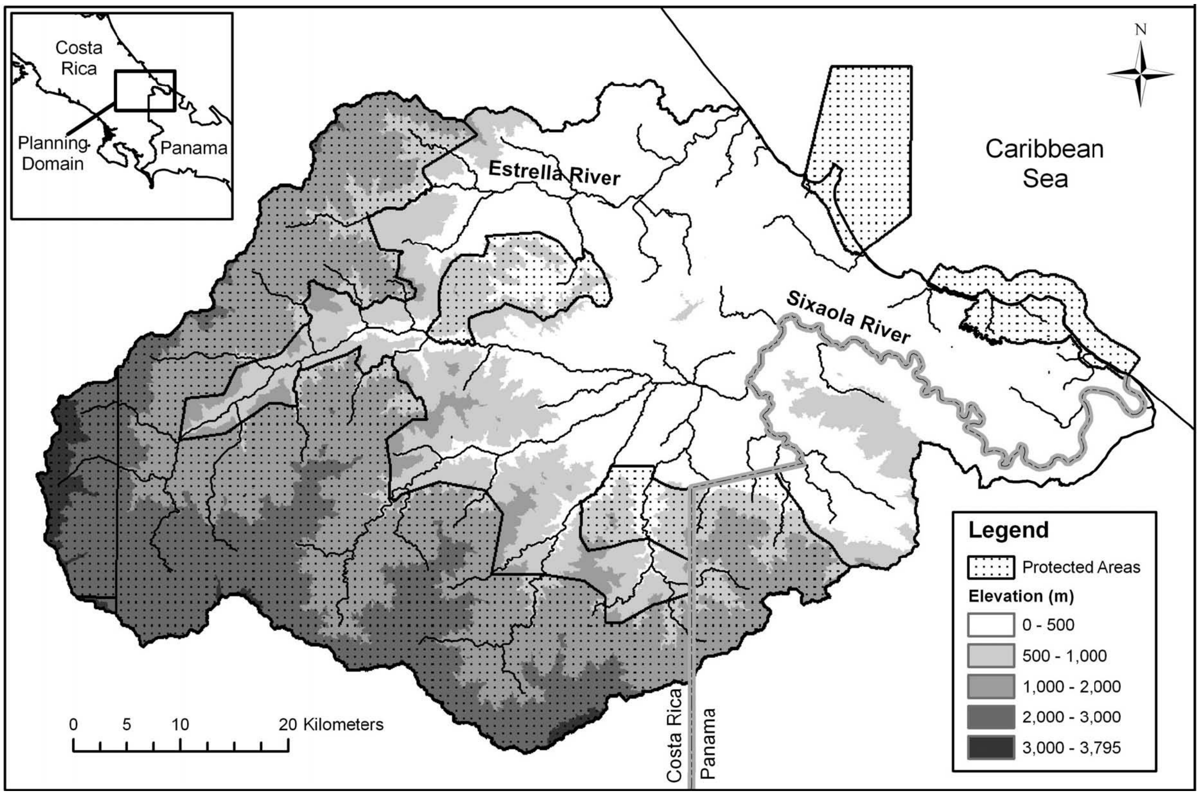


Figure 2. Map of an example planning domain on the Caribbean slope of Costa Rica and Panama.



DISSERTATION CONCLUSIONS

In these four chapters we have taken a “step down” approach to conservation planning across spatial and thematic scales. The global scale is an important first step as it sets the context by identifying, in this case, the species most in need of conservation attention to prevent future extinctions. By collecting both spatial and thematic information for each species we then conduct global scale analysis to identify where in the world most threatened species exist and where the threats are distributed. Because there are no sufficient resources to conserve all species across all regions, this global analysis sets the context for determine where to focus limited resources to save the most species. However because we collected data at a species scale, we can also identify where species specific efforts can be focused, or where we might be able to focus on threats such as by-catch and overharvesting. Therefore at the global scale, we can frame our conservation question in terms of where to focus. However the means for conservation will vary across the globe, as will the tools available to influence policy and management. Using the global dataset to inform decision on where to focus takes us one step closer to knowing how.

At regional and national scales, policy and management tools are important for resource conservation. In many cases protected areas and legislation are already in place, and conservation planning can work within an existing framework. In this case our study area is both a Biosphere Reserve and International Peace Park (between Costa Rica and Panama), but the policies in place which affect the site are national. Therefore we focused our efforts on Costa Rica such that we could make recommendations which could influence management of La Amistad National Park and its environs. However at the regional scale we are also confronted with the explicit historical context which has lead to the current distribution of species. While at the global scale habitat fragmentation is not visible, at the regional and landscape scales it defines the patterns in species distributions, abundance and diversity. Thus when we shift from the global to regional scales we are presented with some measurable ecosystem and anthropogenic features – cities, towns, protected areas, forests, rivers, etc.- and we can begin to focus analysis on the specific issue influencing the region and produce qualitative analysis.

Habitat loss and degradation, at the global scale, affect 40% of all mammals. However at the regional and landscape scales habitat loss is preventable but not reversible in the short term. As we scale down our planning and analysis we inherit more and more of the local context. Whereas we can develop policy and incentives to slow down habitat loss and even to begin the process of restoration – the current configuration of species communities is largely based on what is already remaining and thus recovery can be challenging. In the case of the Talamancas, it is too late to save Jaguar in the surrounding lowlands. Although they are predominately lowlands species, their suitable habitat has been converted to a human dominated landscape and that is the context we are left to work with today. In the remnants of the Caribbean lowland forests, conservation efforts are best focused on community education so that the next generation of land owners can make more educated decisions about their land use practices. In addition, in the human dominated areas it important to link conservation efforts to ecosystems services so that people see a benefit from their actions. This does not mean that we should abandon conservation efforts or large mammals which cannot tolerate humans however; it means that we need to build capacity in the stewards of the remaining Jaguar habitats so that their habitat does not become more reduced in the future.

Hunting is a global issue, affecting approximately 17% of all mammals – but in most cases focused on large mammals. At the global scale we see the effects of hunting across all mammals, and we can see some global trends focusing on SE Asia, Central Africa and the Andes and Amazon Basin. Each of these regions has very different issues, all related to hunting. In SE Asia, species are being hunted to extinction for trade in traditional medicines and for food. In Africa, “bush meat” hunting is driven by a local need for protein sources not available elsewhere. In both of these cases overpopulation and health concerns make for a very different problem than in the Talamanca Mountains. The Talamancas are already a habitat island due to deforestation, and as most of the lowlands have been deforested many of the large mammals remain in marginally suitable habitats. At the regional scale illegal hunting is occurring in the National Parks for sport and for economic gain, very rarely for subsistence. The persistence of the hunting problem is not due to current policies but to the lack of enforcement. The largest National Park in Costa Rica, La Amistad, also has the least amount of resources to protect wildlife as it is off the tourist track. Cahuita National Park, a tiny park on the Caribbean which receives many visitors from cruise ships, has more park guards than the massive La Amistad. Where local officials have tried to enforce the law, communities have turned against them and threatened them. Since the beginning of this study two guard stations were shut down, and today almost all of the guard stations are outside the park. At the regional scale, if hunting is not taken seriously by government authorities, it will result in continued extirpation of large mammals, in the same way the Giant Anteater has already been lost.

In conclusion, we feel there is synergy between scales of conservation, and that all too often projects do not take into account the context and role that scale plays in ecosystems and species. Regional and landscape projects greatly benefit from knowing the global context of the species they are working to conserve. This global context can also help us make decisions about when and where to focus resources. If scarce resources are available then efforts are best focused on what makes an area unique, as in the case we describe herein with Jaguar. Globally to ensure Jaguar does not go extinct we need to retain it across the regions where it is now found. Once ranging from the southern United States to Argentina, the global stronghold for the species is currently the Amazon Basin. However it has disappeared from much of its former range, including the majority of Central America. Therefore at the regional scale, Jaguar conservation in the Talamancas is a priority – along with other large mammals no longer found in the surrounding lowlands. However at the landscape scale in the Talamanca-Caribe, efforts are best focused on smaller species which are unique to the area. In human dominated landscapes we have only the pieces of the puzzle that we are given to work with, and at this scale conservation has to fully engage the human component and work to curb the social norms which created the current landscape context so that the next generation of local decision makers is fully informed about the consequences of deforestation and species loss both to ecosystem and human health.