CORRELATOS BIOLÓGICOS DEL RIESGO DE DECLINACIÓN DE LOS MAMÍFEROS BOLIVIANOS: ESTABLECIENDO PRIORIDADES DE CONSERVACIÓN

Tesis

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INFORME DE APROBACIÓN

Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Magíster presentada por el candidato:

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DEDICATORIA

A mis abuelos, Alicia y Oscar, cuyas historias sobre su
andar por el monte y encuentros con el jucumari,
me introdujeron en el camino de la Biología.

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RESUMEN

Las crecientes listas de especies amenazadas debido al impacto del hombre en los ecosistemas de todo el mundo, han alentado el desarrollo de análisis comparativos con el fin de dilucidar ¿porqué algunas especies son más propensas a la extinción que otras? Entendiendo los factores y procesos relacionados con la vulnerabilidad de las especies a la declinación podría ofrecer una oportunidad para desarrollar estrategias de conservación preventivas. Estos análisis comparativos son de especial interés a escala nacional porque a esa escala se desarrollan la mayoría de los esfuerzos de conservación. Evaluamos la relación entre rasgos de historias de vida y ecológicos de los mamíferos bolivianos con su tendencia poblacional, con el propósito de: a) entender la vulnerabilidad de los mamíferos a escala nacional y b) para predecir la tendencia poblacional de especies poco conocidas o no evaluadas. Encontramos que el riesgo de declinación no está distribuido al azar entre los órdenes de mamíferos de Bolivia. Primates, Cetacea-Artiodactyla-Perissodactyla, Carnivora y Cingulata tienen más especies en declinación. Sin embargo, Rodentia-Lagomorpha y Chiroptera tienen menos especies de lo esperado por azar. Nuestros análisis mostraron que el riesgo de declinación está determinado por múltiples rasgos biológicos. Los mamíferos voladores tienen la probabilidad más baja de declinar, mientras que los mamíferos terrestres no voladores tienen la probabilidad más elevada (> 5,6 kg). Entre los mamíferos pequeños a medianos (<5,6 kg) la probabilidad de declinar depende de la interacción entre la amplitud de hábitat, especialización de dieta, tamaño de camada y el rango geográfico. Finalmente, pudimos predecir la tendencia poblacional de 63 especies poco conocidas, de las cuales 35 estarían en declinación. Encontramos un fuerte apoyo para rasgos consistentes como predictores en estudios previos. Sin embargo, nuestros análisis revelaron además interacción y efectos no lineales entre diferentes atributos con el riesgo de declinación a escala nacional.

Palabras clave: Vulnerabilidad de las especies, declinación, modelos Random Forest, predicción de la tendencia poblacional

ABSTRACT

The growing lists of endangered species due to the human impact over all ecosystems worldwide have encouraged the development and use of comparative analyses to elucidate why some species are more prone to extinction than others. By understanding factors and processes related to species vulnerability to decline might provide an opportunity to develop preventive conservation strategies. Such comparative analyses are of special concern at national scales because these are the scales at which most of the conservation initiatives take place. We tested for correlates of life history and ecological traits with the population trend of the Bolivian mammals, in order to: a) understand species vulnerability at a national scale and b) to predict the population trend for poorly known or non-evaluated species. We found that the risk of decline is not randomly distributed among orders of the Bolivian mammals. Primates, Cetacea-Artiodactyla-Perissodactyla, Carnivora and Cingulata have grater proportions of declining species. However, Rodentia-Lagomorpha and Chiroptera have less declining species than expected by chance, causing the observed heterogeneity. Our analysis showed that the risk of decline is determined by multiple biological traits. Volant mammals have the lowest probability of decline, while terrestrial large-sized mammals (> 5.6 kg) have a greater risk. Among small-medium sized mammals (< 5.6 kg) probability of decline depends on the interaction between habitat breadth, diet breadth, litter size and geographic range. Finally, we predicted the population trend for 63 unknown-trend species, of which 35 are declining. We found strong support for consistent predictor traits previously related to extinction risk in mammals. However our analyses go beyond by showing important interacting and non-linear effects of life history traits on the risk of decline among mammals at a national scale.

Key words: species vulnerability, decline, random forest, predicted population trend

BIOLOGICAL CORRELATES OF THE RISK OF DECLINE AMONG THE BOLIVIAN MAMMALS:

SETTING CONSERVATION PRIORITIES

Introduction

Biodiversity is facing increasingly intense pressures from human activities worldwide (Foley et al. 2005). Despite the conservation efforts deployed to date, rate of its loss seems unabated (Butchart et al. 2010; Rands et al. 2010). This fact is reflected in the growing lists of endangered species in most countries and regions worldwide (Baillie et al. 2004; Vié et al. 2009). To deal with this threat, during the last decade conservationists have focused their work in developing comparative studies of extinction risk in order to understand why some species are more vulnerable to decline, and hence more prone to extinction than others (Owens & Bennett 2000; Purvis et al. 2000a; Jones et al. 2003; Reynolds et al. 2005; Jones et al. 2006; Bielby et al. 2008; Cardillo et al. 2008; Davidson et al. 2009; Gonzales-Suarez & Revilla 2013). Elucidating factors and processes related to species vulnerability to decline might provide an opportunity to develop preventive and proactive conservation strategies to reduce their populations at long-term (Soulé 1986; Fisher & Owens 2004; Cardillo et al. 2006; Rondinini et al. 2011). Furthermore, these correlates of decline could be used to project or predict the status of species not actually evaluated or for which there is no enough information (Cardillo et al. 2006; Davidson et al. 2009; Murray et al. 2011; Pocock 2011). Having a predictive capacity against extinction risk is central in conservation biology (Soulé 1986; Fisher & Owens 2004; Evans et al. 2013), because it could allows us to infer the declining risk for insufficiently known species or for those not yet declining, and thus, to take concrete actions to prevent their disappearance (Cardillo & Meijaard 2012). Predictability becomes more important as we still ignore the current status of extant populations or the distribution range dynamics for an important fraction of species; even in well known charismatic taxa data lacking is still recurrent, in mammals for example 15.2% of the species are regarded as data deficient, 19% of reptiles and 24% of amphibians (Schipper et al. 2008; Vie et al. 2009).

Extinction risk is not randomly distributed among species (Bennett & Owens 1997; Russell et al. 1998; Thomas 2008) and vulnerability has been associated to different intrinsic traits of species (reviewed in: Purvis et al. 2000b; Reynolds 2005; Fisher & Owens 2004). Among mammals in particular, large body size, slow life histories, niche specialization and small geographic range size have been correlated with higher extinction risk, either at global (Purvis et al. 2000a; Davidson et al. 2009, Davidson et al, 2012, Gonzales-Suarez & Revilla 2013) or regional (Brashares 2003; Fisher et al. 2003; Collen et al. 2006) scales.

Comparative analyses at broader scales can help to identify general or consistent traits associated with species vulnerability. However, in order to obtain more precise explanatory patterns on the species risk, due to the idiosyncratic variation of drivers and threats acting over compositionally different assemblages (Fritz et al. 2009; Pocock 2011), it is also necessary to focus analyses on narrower scales (Fisher & Owens 2004; Cardillo et al. 2008; Davies et al. 2008). Geographically narrower correlates of the risk of decline might also improve our capability to assess the state of non-evaluated species or those insufficiently known (e.g. Murray et al. 2011). The more precise outcomes and predictions are achieved in comparative analyses of vulnerability, the more helpful they might be to identify specific targets and priorities (Cardillo & Meijaard 2012), which is especially relevant for developing countries where limited resources availability defines the allocation of specific conservation interventions (Wilson et al. 2011).

Here we examined the taxonomic distribution pattern of species decline and tested for life history and ecological correlates of the risk of decline among the Bolivian mammals, in order to elucidate the role of biological traits in predisposing mammalian species to decline at a national level. Initially, we contrasted the taxonomic distribution of the risk of decline against a null-hypothesis of a random distribution of declining species among orders. We therefore, expected to find a strong relationship of higher probabilities of decline with larger species, those with wider geographic range, broader home ranges, higher trophic level or slow reproductive potential or lower habitat breadth, in contrast to species with opposite ecologies. Further, we aimed to predict the population trend for poorly known species or those not actually evaluated. Bolivia has a highly diverse mammalian fauna, occupies the ninth place in the world by its richness and the fourth in South America and a representative fraction of the species are enough known on their biology and distribution to make this analysis possible (Aguirre 2007; MMAyA 2009; Wallace et al. 2010). Since lack of knowledge is considered a threat source for the Bolivian diversity that prevents the development of biodiversity conservation and management plans (MDSyP 2001), and that 19% of the Bolivian mammals are classified as data deficient and 29% have not been evaluated, any contribution to help guide studies and conservation efforts on poorly known species is of highly relevance.

Methods

Response variable: National Population Trend

As a measure of the species vulnerability, we considered the "national population trend" classification (e.g. Bielby et al. 2008; Murray et al. 2011; Gonzales-Suarez & Revilla 2013), from the last assessment process of endangered species of the Bolivian vertebrates (Aguirre et al. 2009). Population trend assessment classified species into two categories: "declining" or "stable". The former comprised species whose populations are reducing across the country even at such slow rates that is not enough to qualify as endangered species, while the latter comprised species with apparently constant abundances. Classification was based on both empirical data and expert assessment (Tarifa & Aguirre 2009).

Predictor traits: Biological data collection

We collated data for 11 traits that have been previously used to test for correlates in extinction risk in mammals (see Cardillo et al. 2008; Davidson et al. 2009; Collen et al. 2011), which are: biological traits (adult body mass), life history traits (litter size, interbirth interval, age at first reproduction), and ecological traits (mode of life, activity cycle, habitat breadth, diet breadth, trophic level, home range size and geographic range size). Traits data were extracted from published information on Bolivian mammals (Anderson 1997; Aguirre 2007; Wallace et al. 2010) and the global database PanTheria (Jones et al. 2009). Habitat breadth was measured as the number of all ecoregions which any given species inhabits (*sensu* Ibisch et al. 2003). As a measure of geographic range size we considered the extent of occurrence (EOO), measured as the minimum convex polygon that encompasses known points of occurrence for each species. For both geographic variables occurrence points were collated from national databases (Anderson 1997; PCMB 2012; Wallace et al. 2013) and the largest open access international repository of point locations for mammals, the Global Biodiversity Information Facility (GBIF 2013). All estimations were performed in ArcGis10.1.

Because data missing is highly recurrent in the life history knowledge along mammals (Jones et al. 2009), as in our data set (Supporting Information), deleting any species with at least one missing trait could strongly affect our analysis due to the highly biased loss of information, we know far more about some taxa (e.g. primates and carnivores) than others (rodents and bats) (Cardillo et al. 2005, 2006, 2008). Hence, we applied multiple imputation algorithms based on predictive mean matching for continuous variables and proportional odds models for categorical ordered variables (e.g. Fisher et al. 2003; Murray et al. 2011) to impute missing traits-values of species inside each order. We restricted the data imputation process at an order level due to the non-random pattern of data missing in mammals (Gonzales-Suarez et al. 2012). We used the R package "mice" for imputation, which is based on multiple imputations by chained equations (van Buuren & Groothius-Oudshoorn 2011).

Non-random distribution of declining risk

In order to test if declining risk is randomly distributed among taxonomic orders of the Bolivian mammals, we evaluated the bias between observed and expected frequencies of species that have a declining population trend among orders, assuming that the expected number of declining species is proportional to the total percentage of declining species in Bolivia. We tested departures from randomness through a G-test of goodness of fit and a posterior heterogeneity analysis (Dytham 2011, Zar 2010) to identify those orders departed from randomness (Russell et al. 1998). Orders Lagomorpha, Paucituberculata, Perisodactyla and Cetacea were grouped with Rodentia, Didelphimorphia and Artiodactyla respectively, because they are monotypic and to meet the statistical requirements of the G-test (Dytham 2011; Zar 2010).

Modelling approach

To model the population trend of the Bolivian mammals as a function of life history and ecological traits we used the Random Forest models for classification (Breiman 2001). RF is a statistical ensemble learning technique that combines the classification power of hundreds of independent bootstrapped classification trees to improve predictions accuracy and stability by reducing the inherent bias in the data and correlation among predictors (Cutler et al. 2007). Tree-based techniques have proved to be more robust for predictive modeling in comparative analyses of extinction risk (e.g. Sullivan et al. 2006; Davidson et al. 2009, 2012; Burton et al. 2011; Murray et al. 2011). Unlike classical regression methods RF models do not require distributional assumptions neither data independence, thus are a good alternative over phylogenetic contrasts-based models which can over-correct the non-independence among variables that are not necessarily of an evolutive nature (see Sullivan et al. 2006; Bielby et al. 2010; Burton et al. 2011). Additionally, this modelling technique is able to disentangle nonlinear phenomena and context-dependent interactions between predictor variables (Cutler et al. 2007; Davidson et al. 2009).

We built our model using the algorithm implemented in the "randomForest" package (Liaw and Wiener, 2002) for the R environment (R Core Team, 2013), based on 5000 trees. We assessed predictor importance as the mean decrease of accuracy when values of a given predictor are permuted. Model accuracy was quantified using: the overall error rate (the out of bag classification error), the percentage of species correctly classified and the Cohen's Kappa statistic of agreement (Breiman 2001; Gamer et al. 2013). We also developed partial dependence plots of single traits to show their effects on the probability of decline in the RF model (Cutler et al. 2007). Additionally, to visualize relationships among predictor traits we built a single Classification Tree model using the "rpart" package in R (Therneau et al. 2013).

We followed a two-steps process for modelling and predicting the risk of decline among the Bolivian mammals. As a first step we used only species with the response variable (stable or declining), in order to built an explanatory model of the risk of decline. Secondly, once we fitted the final explanatory model we incorporated a set of species without the response variable (unknown-trend species) in order to predict their most likely population trend according to their ecology.

Results

Non-random declining risk

Of the 389 mammalian species currently recognized for Bolivia, 275 (71%) have been classified according to their population trend. Of these, 84 species (30.5%) have a declining trend, 106 (38.5%) are stable and 85 (31.0%) are classified as unknown trend species because there is no enough information to estimate or even infer their trend. The 114 remaining Bolivian mammals have not been evaluated (Aguirre et al. 2007; MMAyA 2009).

In terms of the number of declining species, orders with the highest risk are Cingulata (91.0%), Cetacea-Artiodactyla-Perisodactyla (85.7%), Primates (71.4%) and Carnivora (63.0%). Whereas Chiroptera, Pilosa, Rodentia-Lagomorpha and Didelphimorphia-Paucituberculata have a lower number of declining species (8.1%, 20.0%, 22.0 % & 33.3% respectively).

However, declining risk as a measure of species vulnerability at a national scale, do not occur at random among taxonomic orders of the Bolivian mammals. When we consider the expected number of declining species for each order, the observed number of declining species per order differs from random and are highly heterogeneous ($G = 31.27$; $df = 7$; $p < 0.0001$) (Figure 1). Orders holding more declining species than expected by chance are Primates, Cetacea-Artiodactyla-Perisodactyla group, Carnivora and Cingulata. Conversely, Rodentia-Lagomorpha and Chiroptera have a disproportionately low number of declining species. Both later orders are also responsible of the observed heterogeneity. Once they are excluded from the analysis heterogeneity is no longer significant ($G = 0.31$; $df = 5$; $p = 0.5$), because the expected percentage of declining species increases up to 61.8%. This result lead us to test for correlations of different life history traits that explained the declining risk among the Bolivian mammals.

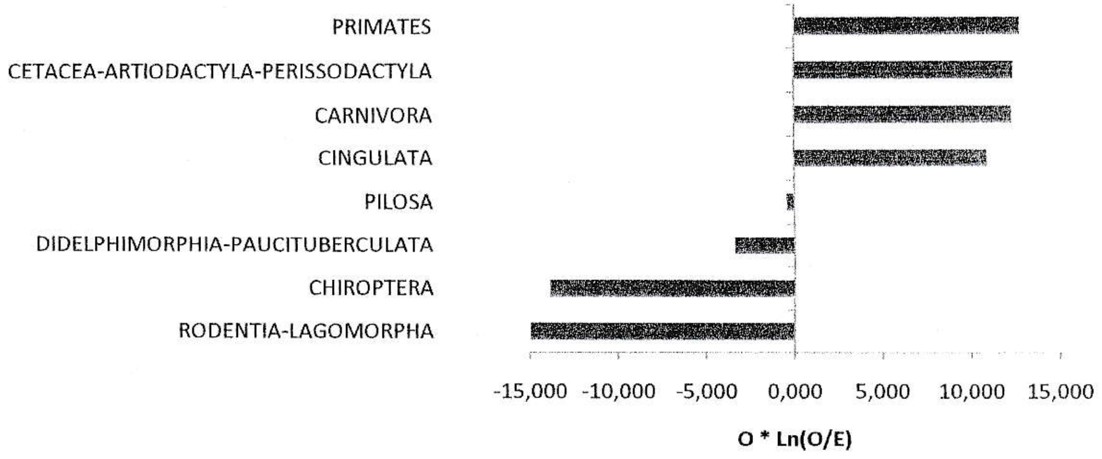

Figure 1. Biases in the number of declining species among taxonomic orders of the Bolivian mammals. Bars size denote contribution of each order to the overall G value.

Predicting the risk of decline

We modelled the population decline risk at a national level using life history and ecological traits of 185 Bolivian mammals for which we were able to estimate the geographic range size (Supporting Information). Our overall Random Forest model classified correctly 78% (143 species) of the Bolivian mammals against their observed population trend (Cohen's Kappa = 0.65, $P < 0.001$), therefore the error rate of the model (22.7% $\mathrm{OOB}_{\mathrm{ERROR}}$) provided 42 misclassified species. Declining species had the highest percentage of correctly classified species at 80.0%, while the percentage of stable species correctly classified was 76.7% (Supporting Information).

Among the misclassified species, 25 currently listed as "stable" were identified declining suggesting that, according to their ecological traits, these species should have a greater risk of decline than hitherto recognized. On the other hand, 17 species listed as "declining" were predicted to be "stable". These misclassified species do not appear to be phylogenetically biased in our model, since they embrace different orders and families (Supporting Information).

Further, using the explanatory model of the risk of decline we were able to predict the population trend for 63 unknown-trend species with geographic range size (EOO). Of these, 35 species were predicted to be declining and 28 were predicted to be stable (Supporting Information).

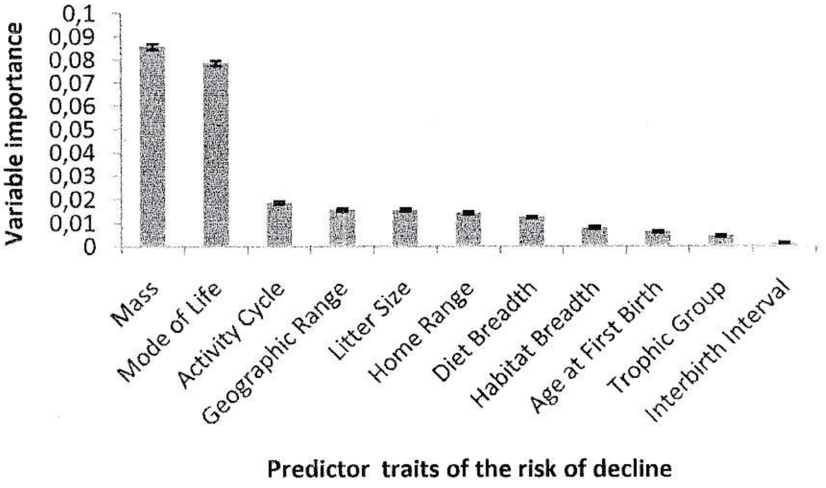

Figure 2. Relative importance ranking of life history and ecological predictors in the Random Forest model. The importance of each variable was calculated as the mean decrease of accuracy when the out-of-bag (OOB) data of the target variable was randomly permuted and passed down again on each tree of the forest. Error bars denote the standard error of the raw variable importance across the 5000 trees. Differences between predictors were estimated by pair-wise two tailed z-test (α = 0.05).

Traits correlated with the risk of decline

Body mass and mode of life were identified as the most important predictor traits of decline risk in the Random Forest model (Figure 2). Although of low importance, other traits also accounted for the risk of decline, namely geographic range (EOO), activity cycle, litter size, home range, diet breadth and habitat breadth (Figure 2). These traits were confirmed in the single Classification Tree model (CT) as important predictors (Supporting Information). Habitat breadth, age at first birth, trophic group and inter-birth interval were consistently the least contributing predictors in both models.

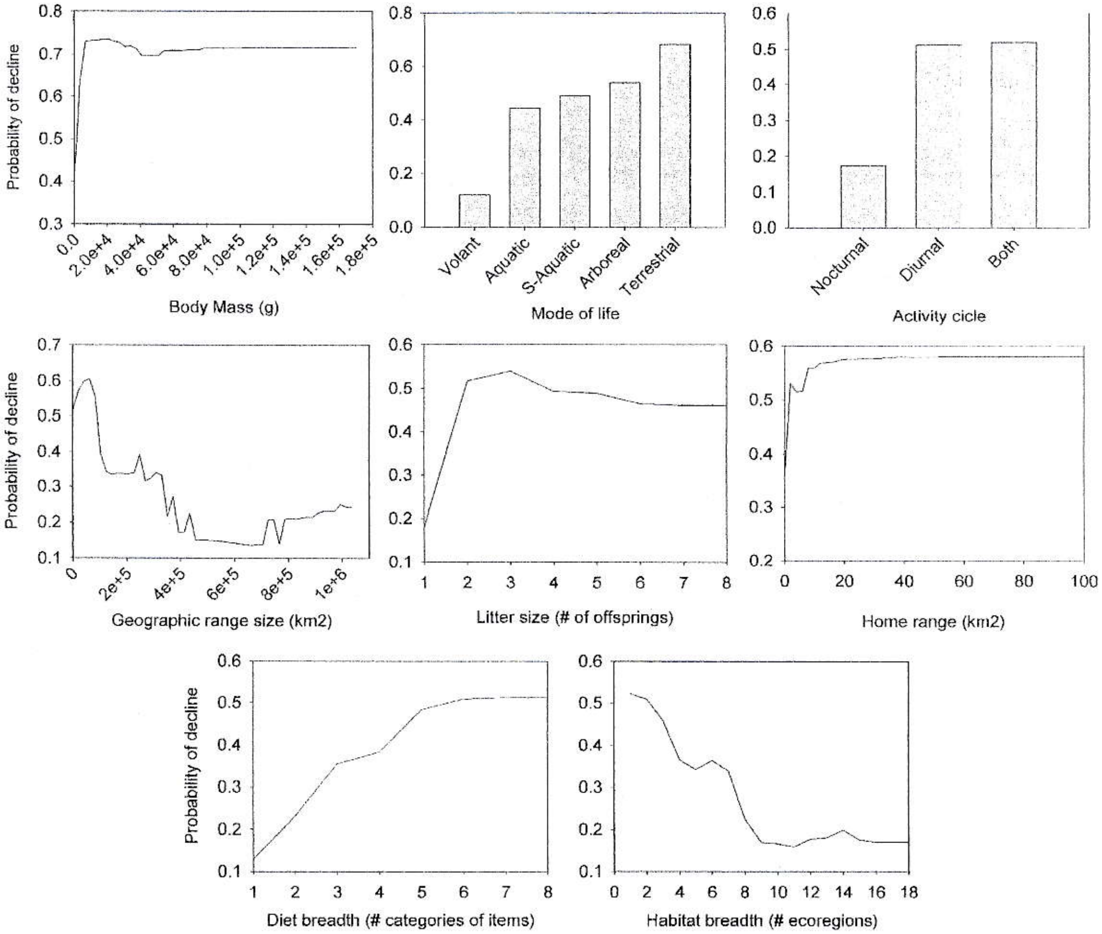

Figure 3. Partial dependence plots of the probability of decline as a function of single predictor traits among the Bolivian mammals.

Partial dependence of key predictors in the model showed mainly non-linear effects of individual traits on species probability of decline (Figure 3). The probability of decline increased abruptly at low values of body mass and home range size. Mode of life and activity cycle had a similar effect on declining risk. Volant and nocturnal mammals had the lowest probability of decline while terrestrial, arboreal and diurnal mammals are more likely to be declining. Diet breadth showed a positive relationship with probability of decline, indicating that generalist species are more likely to have a declining trend. It is noteworthy that the curve reached the asymptote around five categories of prey items in the species diet. Geographic range size showed a negative relationship with declining risk, where species with small ranges (up to 200,000 km^2) are more likely to be declining.

On the other hand, litter size showed a similar pattern, species with two or more offspring had a higher probability of decline whereas species with only one offspring should be the less vulnerable.

Our single CT model revealed "mode of life" as the basal major splitting trait, which placed volant mammals alone in the less-risk right branch of the tree and terrestrial, arboreal, semi-aquatic and aquatic mammals together in the left high-risk branch (Figure 4). Furthermore, on the first branch, probability of decline in bats was associated with geographic range size. Bat species with intermediate ranges (34,615 $km^2 \leq x \leq 85{,}446$ km^2) had a higher risk of decline. On the second main branch non-volant species were classified according to their body mass. Larger mammals (≥ 5.6 kg) exhibit a greater probability of decline, only two species of 35 were stable (Figure 3, node 19). Among the small and medium sized mammals CT model revealed three different pathways to decline depending on the interaction between habitat and diet breadth, interbirth interval, geographic range size and trophic group. Species with a narrow habitat breadth (node 18) or a wide diet breadth (node 17) have a greater probability of decline. Whereas of the remaining species with narrow diet breadth, those with medium to long periods between births, with less than 560,000 km^2 of distribution and being herbivorous or carnivorous, which can be considered as a trophic specialists, are also declining (node 16).

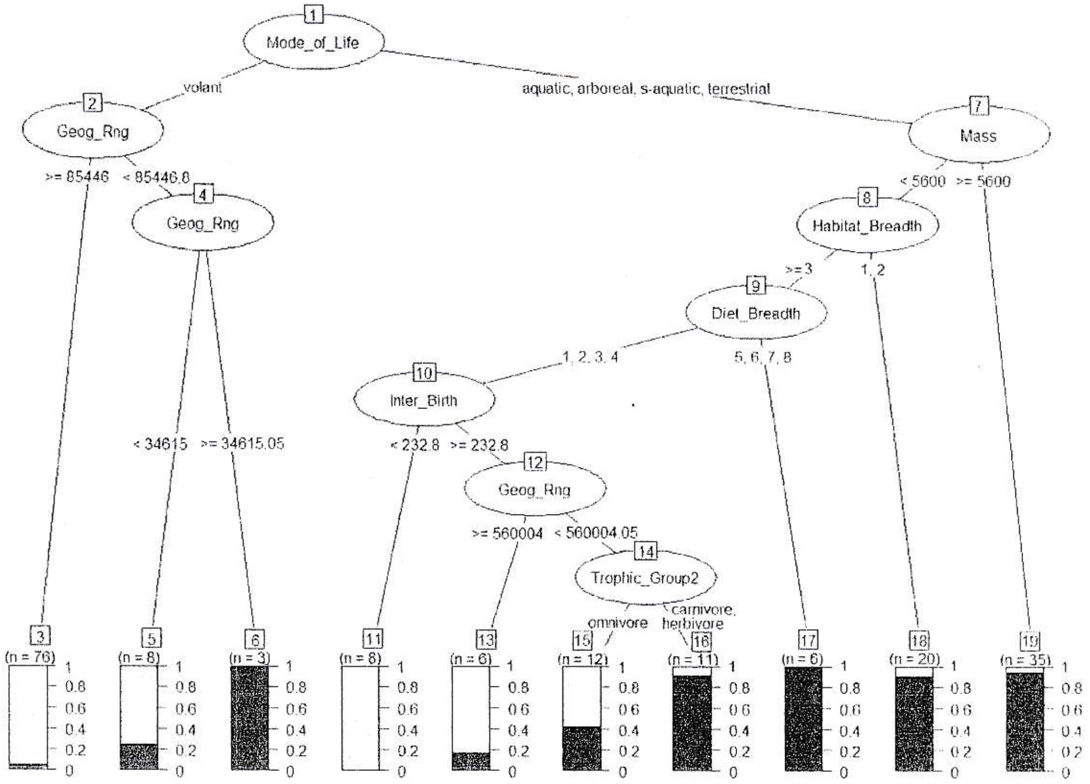

Figure 4. Classification tree of the risk of decline among the Bolivian mammals based on species biological and ecological traits. Inner nodes (ovals) indicate the splitting traits used to classify the species. Numbers on the respective branches are threshold values of each trait. Black bars denote the proportion (probability) of declining species on terminal nodes. *n* is the number of species in each terminal node. Nodes numbers, above ovals or bars, are indicated for reference in text. Thresholds under Habitat breadth and diet breadth indicate the number of ecoregions and prey item types respectively. Geog_Rng = geographic range size, Inter_Birth = interbirth interval.

In order to evaluate if "mode of life" importance value is merely an artifice of the analysis due to the high proportion of bats being stable, we repeated both RF and CT analysis excluding this trait. Results were highly consistent with the all-traits models in terms of accuracy, sensitivity and specificity (Supporting Information). The only difference was evident in the CT model, where body mass appeared as the first splitting trait, separating small sized mammals (< 80 gr) as the less vulnerable group and medium and large sized mammals (> 80gr) as the most vulnerable (Supporting Information).

Further, to test the importance of phylogeny in the risk of decline among the Bolivian mammals, we run RF and CT models including Order as a taxonomic grouping factor. Both models performed with similar accuracy compared to our first models. In these analyses, Order appeared as the second most important predictor of declining trend and replaced mode of life as the first splitting variable in the CT model (Supporting Information). However, predictions of the population trend for species in both the learning sample and the unknown trend sample, through the RF model were substantially the same in comparison to the first analysis.

Discussion

Distribution of the risk of decline

The risk of decline is non-randomly distributed across taxa of the Bolivian mammals, as previously shown at broader scales (Russell et al. 1998; Jones et al. 2003). Medium and large sized mammals appeared to be more susceptible to decline, in contrast to smaller species (rodents and chiropterans). However, what is more relevant from our analysis is that non-randomness is caused only by those orders holding less declining species and, if they were excluded from the analysis the expected percentage of declining species increases from 30.5% to 61.8%, which suggests that vulnerability and thus extinction proneness are more widespread among the Bolivian mammals.

The biology of the risk of decline

Our overall results reveal that multiple biological and ecological traits have an effect in determining the risk of decline in mammals at a national scale. We found strong support for consistent traits associated with species extinction risk among mammals at global (Purvis et al. 2000a; Jones et al. 2003; Cardillo et al. 2008; Gonzáles-Suárez & Revilla 2013) or local scale (Brashares 2003; Collen et al. 2006), such as body mass, geographic range size, generation time and home range. However, our results go beyond previous comparative studies in that we also found evidence for mode of life, habitat breadth, diet breadth and litter size as correlated traits with the risk of decline. Together, these traits emphasise the importance of life history, niche specialization and distribution in determining the species vulnerability. Moreover, our results differ from studies that used quantitative measures of declining rates of local mammalian populations (Mace et al. 2010; Collen et al. 2011), which found that risk of decline correlates with environmental factors instead of biological traits.

Another main difference with studies that compared extinction risk between large and small-sized mammals at a broader scope (Cardillo 2003; Cardillo et al. 2005; Davidson et al. 2009), is that we found strong support for life history correlates among small and medium sized mammals. Our models showed that their life history (inter birth interval) as well as their ecology (diet breath, habitat breath) predispose them to have a declining trend (Figure 3).

Similar to Davidson et al. (2009, 2012), our analyses also demonstrated that species key traits have interacting effects and, more important, non-linear relationships on the risk of decline. Mode of life and body mass were the most important predictors because they define the first splits in the classification model and hence define different pathways to decline by interacting with other traits.

The effect of mode of life on the probability of decline and its role as the first splitting variable in our CT model, suggests strong differences in species survival according to their lifestyles (Johnson 2002), as volant mammals are classified as the clade with the lowest probability of decline in contrast to non-volant species (Figure 3). This result is consistent to that found in global analysis of extinction risk in bats. Chiropterans are less prone to extinction than other taxa among mammals and also microchiropterans are less vulnerable than megachiropterans (*Pteropodidadae*) regardless to their body size or other biological traits (Mace & Balmford 2000; Jones et al. 2003; Davidson et al. 2009).

Body mass had also an important effect in declining risk among Bolivian mammals. The partial plot of this trait showed a dichotomous classification pattern suggesting that small increases in this variable confers species a greater vulnerability. The size threshold of 5.6 kg we found, agrees with previous studies of extinction risk in mammals at a global scale (Cardillo et al. 2005; Davidson et al. 2009; Gonzales-Suáres & Revilla 2013). For example, Davidson et al. (2009) found that extinction risk in mammals rise firstly based on body mass classification, a threshold of 5.5 kg separated larger mammals and small sized mammals, the former being more likely to go extinct. Similarly, Cardillo et al. (2005) found a critical value of 3 kg of body size above which species has a greater extinction risk. However, unlike Davidson et al. (2009) classification model, ours identified no other biological trait splitting large mammals, suggesting that at a national scale all big herbivores, carnivores and some primates and rodents above the size of a bush dog *(Spheotos venaticus)* are more susceptible to decline (94% of probability) mainly because of their size.

This finding reflects the impact of threatening processes like subsistence hunting, commercial exploitation or persecution due to human-wildlife conflicts, imposed to large sized species. Either because of the reduced reproductive potential, slow life histories, high energetic budgets or failure to recovery after protection, larger mammals are more sensitive to these factors (Bodmer et al. 1997; Purvis et al. 2000a; Carbone et al. 2007; Charnov & Zuo 2011). In the Amazonian and Chacoan lowlands of Bolivia primates (*Alouatta caraya, A. sara, Ateles chamek*) and ungulates (*Ozotoceros bezoarticus, Blastocerus dichotomus, Catagonus wagneri*) are important components in the diet of local indigenous and rural communities (Cuellar & Noss 2003, Townsend & Rumiz 2003), and despite some of them are present in high densities or are widely distributed across the lowlands, their populations are seemed to be declining (Venegas et al. 2007; MMAyA 2009). On the other hand, *Lycalopex culpaeus* and *Puma concolor* exemplify big carnivores having a declining trend regardless of being non-threatened (see Tarifa & Aguirre 2009). Due to the conflict with livestock owners, their populations are estimated under constant decline, especially in the Andean highlands (Tarifa & Aguirre 2009).

Small geographic range size typically has been related to greater extinction and declining risk in mammals because it is related with the species limited ability to withstand environmental stochastic events (Purvis et al. 2000a; Harcourt et al. 2002; Jones et al. 2003; Cardillo et al. 2008; Davidson et al. 2009). Our results support the general effect of this ecological trait on the Bolivian mammal's vulnerability; however, it is more relevant for medium and small sized species according with our CT model. Species such as *Chinchilla chinchilla, Lagotrix cf. cana tschudii, Callicebus aureipalati, Callicebus pallescens* have narrow ranges and are under hunting pressure (MMAyA 2009; Wallace et al. 2010). Among bats for example, species with wider geographic range in the country are less likely to decline (*prob.* < 0.06, node 3), which is consistent with that found by Jones et al. (2003).

We also found strong support for a higher risk of decline due to habitat specialization. Our analyses revealed that this trait is especially relevant for non volant small-medium sized mammals inhabiting one or two habitat types (e.g. *Gracilinanus aceramarcae, Callicebus olallae, Calyptophractus retusus, Abrocoma boliviensis, Oxymycterus hucucha*). This effect of habitat specialization agrees with observed patterns among marsupials and primates at global (Fisher et al. 2003, Harcourt 2002) and regional (Brashares 2003) scales, therefore highlight the intrinsic vulnerability of species adapted or restricted to few habitat types.

Contrary to this result, diet breadth showed the opposite effect as species with a broader number of diet item types seemed to have a greater declining risk. A plausible explanation of this result rises when looking at the species subset identified in the CT model as having a greater risk by diet generalization (> 5 item types in their diet, node 17). Despite their elevated local abundances some of these species are under high pressure of hunting for consumption or trade (*Dasypus novemcinctus, Euphractus sexcinctus*) and/or because are considered crop plagues (*Chaetophractus vellerosus*) (Tarifa & Aguirre 2009, Noss et al. 2008, Cuellar & Noss 2003). On the other hand, *Dasyprocta punctata* shows low densities and small reproductive potential (1 to 3 cubs per litter) (Wallace et al. 2010).

Finally, the counterintuitive effect of litter size observed in the all-species RF model is explained by the fact that the vast majority of bats have only one offspring per litter and because of the high proportion of bats with stable population trend in the model's training sample. Therefore, once we repeated the analyses only for non-volant species litter size effect on declining risk becomes clear (Supporting Information). As predicted by theory species with small litters are more susceptible to decline and to go extinct because they fail to compensate mortality or exploitation rates (Purvis et al. 2000a; Cardillo 2003).

Implications for conservation of the Bolivian mammals

Both predictive outcomes from our Randon Forest models are of highly relevance for the conservation planning of the Bolivian mammals because they provide a species-by-species insight of those that need urgently more attention on the basis of their populations decline. First, among the misclassified species, those actually considered stable but according to their ecologies they should be declining could be reflecting their capability to withstand threats that otherwise could cause their decline. However, in the worst case these species would need conservation initiatives to prevent future declines. On the other hand, species predicted to be stable, but observed declining, suggest that other extrinsic threats that beat their intrinsic resilience, such as climate change, must be affecting them.

Conclusions

Our models revealed that the risk of decline is more complex than the scaling up relationship with body mass or geographic range only, as advanced in previous comparative studies (Purvis et al. 2000a; Cardillo et al. 2005; Collen et al. 2011). At a national scale what makes a species more vulnerable to decline depends also on its life style, habitat specialization, diet generalization and reproductive potential. However and more importantly, our results underpin the interacting effect of multiple traits in determining different pathways of risk. Our models also provided priority species due to their observed trend, as well as about species with a high probability for a future decline.

Since the vast majority of conservation-oriented decisions and strategies are deployed at a national scale, it is of high relevance to elucidate patterns, factors and processes underlying the selectivity of decline among biodiversity at this same scale. By doing this we would be able to better inform (see Cardillo & Meijaard 2012) decision makers and stakeholders (e.g. Painter et al. 2011) about the current and future state of declining species, in order to have a plausible effect on conservation practice.

Supporting Information

Summary of the variables, the response variable and biological traits, and data availability (Appendix S1), accuracy metrics of the Random Forest models and the Classification Tree model (Appendix S2), misclassified species list according to our Random Forest model predictions over the training sample (Appendix S3), predicted population trend species list (Appendix S4), relative importance ranking of predictors in the classification tree model (Appendix S5), classification tree model without "mode of life" (Appendix S6) and partial dependence plots of the RF model only for non-volant mammals (Appendix S7) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Supporting Information

Appendix S1. Summary of life history and ecological traits used to model the risk of decline among the Bolivian mammals. Number of species with known population trend and available data for each predictor trait, number of species with data and for which geographic range size was estimated (species with at least three occurrence points), the relative percentage of species with data in the geographic range-sample (N_{GeoRng} = 248 species) and relative percentage of species in the geographic range-sample for which traits data was imputed.

	N with data available	N from the species with geographic range	% (N_{GeoRng}=248)	% imputed
Response variable				
Population trend	190	185	74.6	0 (excluded)
Intrinsic predictors				
Body mass	348	242	98.4	1.6
Age at first birth	86	82	33.1	66.9
Inter-birth interval	152	138	55.6	44.4
Litter size	250	206	83.1	16.9
Trophic group	281	231	94.4	5.6
Diet breadth	277	227	92.7	7.3
Activity cycle	254	202	83.1	16.9
Mode of life	305	232	94.8	5.2
Home range	91	86	34.7	65.3
Habitat breadth	286	248	100	0
Geographic range	248	248	100	0 (excluded)

Appendix S2. Accuracy metrics of the random forest model used to predict the population trend of the Bolivian mammals (n = 185 species).

	Full traits/species models		**Models without "mode of life"**	
Accuracy metric	**RF**	**CT**	**RF**	**CT**
Error rate	22.16	9.19	22.70	10.20
PCC	77.84	90.81	77.30	89.80
Specificity	76.70	95.15	76.70	94.90
Sensitivity	80.00	85.37	78.05	85.00
Cohen's Kappa (P-value)	0.55 (p<0.001)	0.81 (p<0.001)	0.51 (p<0.001)	0.78 (p<0.001)

PCC is the percentage of species correctly classified by the model. Specificity is the percentage of stable species correctly classified whereas sensitivity is the percentage of declining species correctly classified. The Cohen's Kappa value reflects the measure of agreement between actual population trend and predicted trend by the model corrected for agreement by chance.

Appendix S3. Misclassified species list according to the full traits/species Random-Forest model predictions.

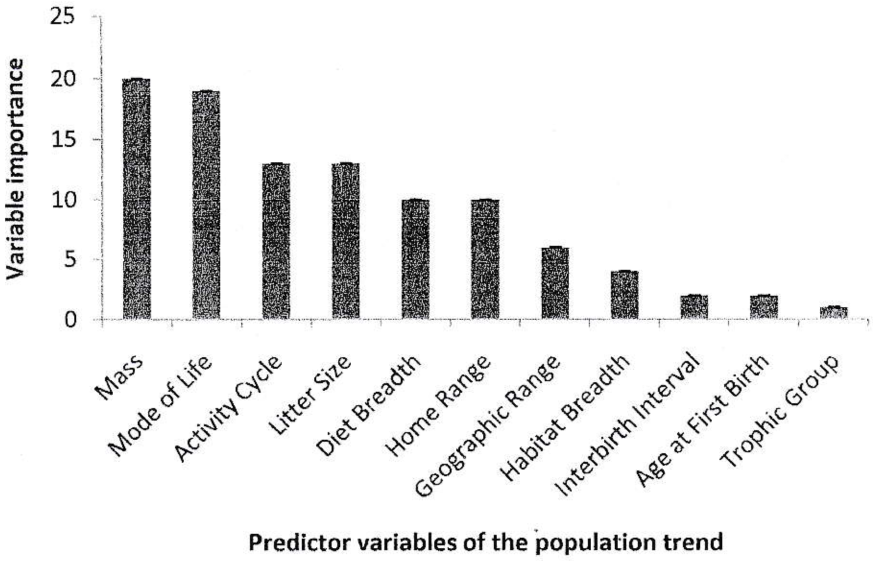
Current Population Trend	Predicted Trend	Order	Family	Species
Stable	Declining	Carnivora	Canidae	*Cerdocyon thous*
		Carnivora	Canidae	*Lycalopex gymnocercus*
		Carnivora	Mustelidae	*Eira barbara*
		Carnivora	Procyonidae	*Bassaricyon alleni*
		Carnivora	Procyonidae	*Potos flavus*
		Artiodactyla	Camelidae	*Vicugna vicugna*
		Chiroptera	Emballonuridae	*Saccopteryx leptura*
		Chiroptera	Phyllostomidae	*Lampronycteris brachyotis*
		Chiroptera	Phyllostomidae	*Mimon crenulatum*
		Didelphimorphia	Didelphidae	*Lutreolina crassicaudata*
		Didelphimorphia	Didelphidae	*Marmosops bishopi*
		Didelphimorphia	Didelphidae	*Marmosops creightoni*
		Didelphimorphia	Didelphidae	*Metachirus nudicaudatus*
		Pilosa	Bradypodidae	*Bradypus variegatus*
		Pilosa	Myrmecophagidae	*Tamandua tetradactyla*
		Primates	Aotidae	*Aotus azarae*
		Primates	Callitrichidae	*Mico melanurus*
		Primates	Cebidae	*Saimiri boliviensis*
		Rodentia	Caviidae	*Cavia tschudii*
		Rodentia	Caviidae	*Galea musteloides*
		Rodentia	Caviidae	*Hydrochoerus hydrochaeris*
		Rodentia	Cricetidae	*Thomasomys ladewi*
		Rodentia	Ctenomyidae	*Ctenomys steinbachi*
		Rodentia	Sciuridae	*Sciurus argentinius*
Declining	Stable	Carnivora	Mephitidae	*Conepatus chinga*
		Chiroptera	Natalidae	*Natalus espiritosantensis*
		Chiroptera	Phyllostomidae	*Anoura caudifer*
		Chiroptera	Phyllostomidae	*Anoura cultrata*
		Chiroptera	Phyllostomidae	*Anoura geoffroyi*
		Chiroptera	Phyllostomidae	*Lophostoma carrikeri*
		Chiroptera	Phyllostomidae	*Micronycteris megalotis*
		Chiroptera	Phyllostomidae	*Platyrrhinus albericoi*
		Chiroptera	Phyllostomidae	*Vampyrum spectrum*
		Chiroptera	Vespertilionidae	*Myotis dinellii*
		Didelphimorphia	Didelphidae	*Caluromys lanatus*
		Didelphimorphia	Didelphidae	*Glironia venusta*
		Didelphimorphia	Didelphidae	*Gracilinanus aceramarcae*
		Didelphimorphia	Didelphidae	*Monodelphis kunsi*
		Rodentia	Chinchillidae	*Chinchilla chinchilla*
		Rodentia	Dasyproctidae	*Dasyprocta punctata*
		Rodentia	Erethizontidae	*Coendou prehensilis*

Appendix S4. Predicted-trend species list according to the explanatory Random Forest model of the risk of decline among the Bolivian mammals.

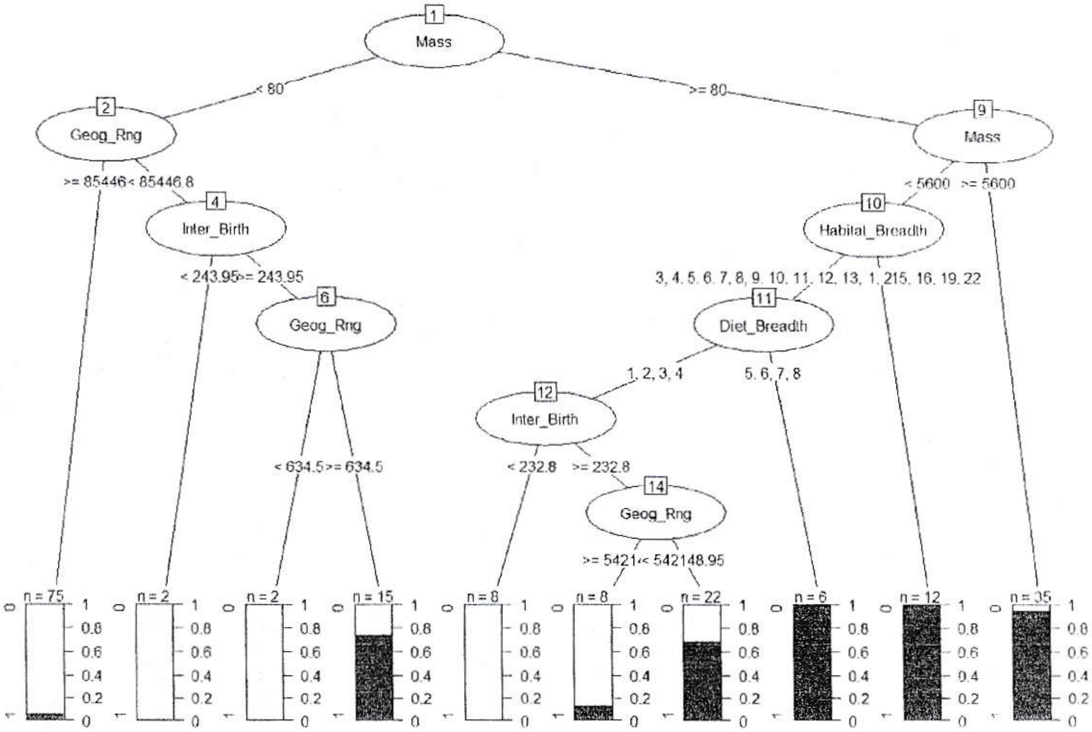
Order	Family	Species	Predicted Trend
Artiodactyla	Cervidae	*Odocoileus peruviana*	declining
Carnivora	Felidae	*Leopardus tigrinus*	declining
Carnivora	Mustelidae	*Galictis cuja*	declining
Carnivora	Mustelidae	*Galictis vittata*	declining
Carnivora	Mustelidae	*Mustela frenata*	declining
Chiroptera	Thyropteridae	*Thyroptera discifera*	declining
Cingulata	Dasypodidae	*Cabassous unicinctus*	declining
Didelphimorphia	Didelphidae	*Cryptonanus unduaviensis*	declining
Didelphimorphia	Didelphidae	*Didelphis marsupialis*	declining
Didelphimorphia	Didelphidae	*Didelphis pernigra*	declining
Didelphimorphia	Didelphidae	*Marmosa regina*	declining
Didelphimorphia	Didelphidae	*Thylamys venustus*	declining
Pilosa	Megalonychidae	*Choloepus hoffmanni*	declining
Primates	Aotidae	*Aotus nigriceps*	declining
Primates	Cebidae	*Cebus albifrons*	declining
Primates	Cebidae	*Cebus libidinosus*	declining
Rodentia	Caviidae	*Dolichotis salinicola*	declining
Rodentia	Chinchillidae	*Lagostomus maximus*	declining
Rodentia	Cricetidae	*Akodon pervalens*	declining
Rodentia	Cricetidae	*Akodon varius*	declining
Rodentia	Cricetidae	*Chinchillula sahamae*	declining
Rodentia	Cricetidae	*Galenomys garleppii*	declining
Rodentia	Cricetidae	*Hylaeamys acritus*	declining
Rodentia	Cricetidae	*Juscelinomys huanchacae*	declining
Rodentia	Cricetidae	*Tapecomys wolffsohni*	declining
Rodentia	Cricetidae	*Thomasomys daphne*	declining
Rodentia	Ctenomyidae	*Ctenomys frater*	declining
Rodentia	Ctenomyidae	*Ctenomys leucodon*	declining
Rodentia	Ctenomyidae	*Ctenomys lewisi*	declining
Rodentia	Cuniculidae	*Cuniculus taczanowskii*	declining
Rodentia	Echimyidae	*Proechimys brevicauda*	declining
Rodentia	Echimyidae	*Proechimys longicaudatus*	declining
Rodentia	Echimyidae	*Proechimys simonsi*	declining
Rodentia	Echimyidae	*Proechimys steerei*	declining
Rodentia	Erethizontidae	*Coendou bicolor*	declining
Carnivora	Felidae	*Puma yagouaroundi*	stable
Chiroptera	Emballonuridae	*Diclidurus albus*	stable

Order	Family	Species	Predicted Trend
Chiroptera	Molossidae	*Cynomops planirostris*	stable
Chiroptera	Molossidae	*Eumops hansae*	stable
Chiroptera	Molossidae	*Eumops perotis*	stable
Chiroptera	Molossidae	*Nyctinomops aurispinosus*	stable
Chiroptera	Molossidae	*Promops centralis*	stable
Chiroptera	Molossidae	*Promops nasutus*	stable
Chiroptera	Mormoopidae	*Pteronotus gymnonotus*	stable
Chiroptera	Mormoopidae	*Pteronotus rubiginosus*	stable
Chiroptera	Phyllostomidae	*Carollia manu*	stable
Chiroptera	Phyllostomidae	*Choeroniscus minor*	stable
Chiroptera	Phyllostomidae	*Dermanura gnoma*	stable
Chiroptera	Phyllostomidae	*Lichonycteris degener*	stable
Chiroptera	Phyllostomidae	*Lionycteris spurrelli*	stable
Chiroptera	Phyllostomidae	*Lonchophylla dekeyseri*	stable
Chiroptera	Phyllostomidae	*Lonchophylla thomasi*	stable
Chiroptera	Phyllostomidae	*Platyrrhinus incarum*	stable
Chiroptera	Phyllostomidae	*Platyrrhinus masu*	stable
Chiroptera	Phyllostomidae	*Platyrrhinus nigellus*	stable
Chiroptera	Thyropteridae	*Thyroptera tricolor*	stable
Chiroptera	Vespertilionidae	*Rhogeessa io*	stable
Didelphimorphia	Didelphidae	*Didelphis albiventris*	stable
Didelphimorphia	Didelphidae	*Marmosops impavidus*	stable
Didelphimorphia	Didelphidae	*Philander canus*	stable
Pilosa	Cyclopedidae	*Cyclopes didactylus*	stable
Rodentia	Caviidae	*Microcavia niata*	stable
Rodentia	Chinchillidae	*Lagidium viscacia*	stable

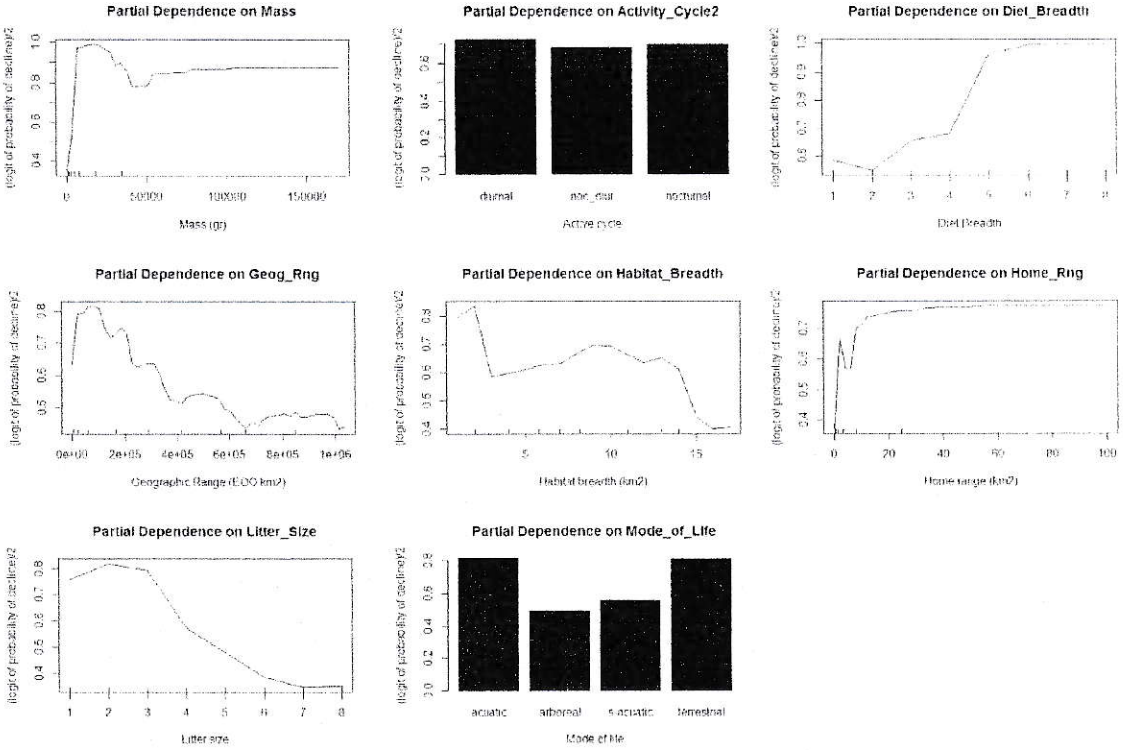
Appendix S5. Relative importance ranking of the life history and ecological predictors in the classification tree model.



Appendix S6. Classification tree of the risk of decline among the Bolivian mammals without the trait "mode of life". Inner nodes (ovals) indicate the splitting traits used to classify the species. Figures on the respective branches are threshold values of each trait. Black bars denote the proportion (probability) of declining species on terminal nodes. Nodes numbers, above ovals or bars, are indicated for reference in text. Thresholds under Habitat breadth and diet breadth indicate number of ecoregions and prey item types respectively. Geog_Rng = geographic range size, Inter_Birth = interbirth interval.



Appendix S7. Partial dependence plots of ecological traits in the RF model only for non-volant mammals of Bolivia.



Partial Dependence on Mass

Partial Dependence on Activity_Cycle2

Partial Dependence on Diet_Breadth

Partial Dependence on Geog_Rng

Partial Dependence on Habitat_Breadth

Partial Dependence on Home_Rng

Partial Dependence on Litter_Size

Partial Dependence on Mode_of_Life