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THE DISAPPEARANCE OF THE JAGUAR

THE POSSIBLE CONSEQUENCES FOR NEOTROPICAL FOREST ECOSYSTEMS

A LITERATURE REVIEW

Daisy van de Biezen

The disappearance of the jaguar (*Panthera onca*) from neotropical forest ecosystems

A qualitative literature review of the possible consequences for ecosystem functioning in neotropical lowland forests

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Preface

This paper is the final paper as part of the graduation phase of the Bachelor's program in Applied Biology at Aeres University of Applied Sciences in Almere, the Netherlands. Throughout my four years in the Applied Biology program, I have had the opportunity to engage in various research projects both locally and internationally, providing me opportunities to better understand the complex system that is the natural world.

I have always had a fascination for tropical ecosystems and the complexity it holds with their immense biodiversity and intertwined relationships between species and their environment. One animal influencing these complex interactions and one that has always amazed me with its looks is the jaguar. The jaguar has always been a species of interest but unfortunately, its elusiveness has led to failed attempts in 2022 of seeing this majestic and stunning apex predator in the wild Peruvian Amazon. I have been wanting to learn more about ecosystems and species interactions. As I delved into the research on the ecological role of a big predator like the jaguar, I found myself captivated by the intricate web of relationships that these apex predators have with their environment. Have you ever wondered what would happen to the delicate ecosystems if the jaguar, one of its apex predators, were to disappear? I surely have. Ever since my trips to the neotropics, the role such a big feline predator may really have, is what piqued my interest in doing this literature review.

I would like to thank Eelco Petstra for his support and guidance throughout the process and for having faith in me doing a literature study, regardless of it being a challenging task. Additionally, I would like to thank everybody who provided me with tips, feedback, and new insights on how to approach this study.

"An understanding of the natural world is a source of not only great curiosity but great fulfillment." – David Attenborough

With kind regards,

Daisy van de Biezen

2 June 2023, Zutphen

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Summary

Residing atop the trophic ladder, the jaguar plays a crucial role in the functioning, stability, and resilience of neotropical forest ecosystems. They influence the entire food web and have wide-ranging effects on various ecological processes. However, jaguars are a highly at-risk and near-threatened species and have been lost over more than half their historical range. The full consequences of their extinction on ecosystems remain unclear due to limited research and complex ecological dynamics. Therefore, there is a pressing need to forecast the implications of their absence as ecosystem drivers for effective conservation planning.

Current literature demonstrates that the absence of jaguars can disrupt the intricate interrelationships among species in the ecosystem. They exert top-down influences on their prey and influence co-occurring predators through interspecific competition. The impacts on predator and prey populations depend on factors such as abundance, density, and socio-ecological characteristics but seem the most pronounced in white-lipped peccaries through over-predation and pumas through competition as jaguars have a competitive dominance over them. The direct and indirect effects of jaguar declines on predators, prey, and the environment are interconnected and can lead to mesopredator release, changes in (native and invasive) prey populations, shifts in co-occurring predator diets, increased disease transmissions, alterations in forest composition, and shifts in prey behavior. It is uncertain whether another predator could completely serve as a surrogate for the jaguar's ecological role. The puma is the closest predator to the jaguar and may partially fill its role through niche expansion and density compensation, but differences in diet and physical characteristics limit its ability to fully compensate.

Trophic cascades such as increased prey populations, behavioral changes, and alterations in forest composition have been observed in the absence of jaguars. However, the occurrence and extent of these cascades depend on various factors and are still subject to research and debate. The interference of anthropogenic factors further complicates the understanding of jaguar influences as their combined impacts can result in divergent outcomes. Anthropogenic factors contribute to both the decline of jaguars and co-occurring species, also causing alterations in ecosystem functioning. It is therefore recommended to continue the monitoring of crash events and changes in the wider terrestrial vertebrate community in areas where jaguars are currently significantly declining. Future research should continue to investigate the consequences of jaguar decline, considering complex interactions and combined effects of multiple species and human disturbance on ecosystems, narrowing knowledge gaps for conservation planning.

Samenvatting

De jaguar speelt een cruciale rol in het functioneren, de stabiliteit en veerkracht van een neotropisch bosecosysteem. De soort beïnvloedt het gehele voedselweb en heeft daarbij grote invloed op ecologische processen. Jaguars staan echter zeer onder druk en zijn uit meer dan de helft van hun oorspronkelijke verspreidingsgebied verdwenen. Vanwege de complexiteit van ecologische relaties binnen ecosystemen, zijn de gevolgen van afwezigheid van jaguar nog onduidelijk. Hierdoor ontstaat een sterke behoefte de effecten van hun afwezigheid te voorspellen voor effectieve beschermingsmaatregelen.

Uit de literatuur blijkt dat de afwezigheid van jaguars de complexe onderlinge relaties tussen soorten in het ecosysteem kan verstoren. Ze hebben een top-down invloed op hun prooidieren en beïnvloeden co-voorkomende predatoren door middel van competitie. De impact op de populaties van predatoren en prooidieren is afhankelijk van factoren zoals abundantie, dichtheid en sociaalecologische kenmerken. De effecten uiten zich onder andere in de vorm van veranderingen binnen prooipopulaties, bossamenstellingen en in prooigedrag. Verder worden toenames gezien in mesopredatoren, overdracht van ziektes en zijn er ook verschuivingen in het dieet van co-voorkomende predatoren waargenomen. Soort-specifiek gezien lijkt de impact het meest uitgesproken te zijn binnen populaties witlippekari's door middel van een grote predatiedruk. Verder is de invloed op poema's groot doordat de jaguar dominant is over deze soort en zo vermijdingsgedrag van poema plaatsvindt. In de afwezigheid van jaguar is poema echter wel een soort met potentie voor het gedeeltelijk vervullen van zijn ecologische rol in de vorm van niche-uitbreiding en dichtheidscompensatie. Verschillen in dieet en fysieke kenmerken beperken echter zijn vermogen om volledig te compenseren.

Trofische cascades, zoals toenemende prooipopulaties en veranderingen in bossamenstelling, zijn aangetoond in de afwezigheid van jaguars. Het optreden en de omvang van deze cascades zijn echter afhankelijk van diverse factoren die door menselijke invloeden kunnen worden versterkt. Dit komt doordat hun gecombineerde impact tot uiteenlopende effecten kunnen leiden. Menselijke invloeden dragen bij aan zowel de achteruitgang van jaguars als andere voorkomende soorten en veroorzaken zo eveneens veranderingen binnen het functioneren van een ecosysteem.

Het wordt aanbevolen om te blijven monitoren in gebieden waar jaguars momenteel aanzienlijk afnemen. Hierbij gaat het met name om het monitoren van crashgebeurtenissen en veranderingen in de brede gemeenschap binnen neotropische bossen. Toekomstige studies moeten worden gericht op het onderzoeken van de gevolgen van de achteruitgang van jaguars, waarbij complexe interacties en gecombineerde effecten van meerdere soorten en menselijke verstoring op ecosystemen worden meegewogen, waardoor kennisleemtes worden verkleind.

1. Introduction

Apex predators play an essential role in an ecosystem because they reside atop the trophic ladder and influence the food web below them (Terborgh & Estes, 2010; Jorge et al., 2013). Terrestrial vertebrate apex predators are large-bodied, allowing them to move across large areas, thus linking the dynamics of seemingly unconnected communities and ecosystems. According to recent ecological research, it is well-recognized that large predators are of great importance for ecosystems in terms of ecosystem functioning, stability, and resilience (Terborgh & Estes, 2010; Ritchie et al., 2012; Ripple et al., 2014). Influencing prey populations (Ripple et al., 2014) and suppressing smaller carnivores (Prugh & Sivy, 2020) are well-known effects. However, the effects large predators have on myriad ecological processes and functioning are often wide-ranging. For example, they can have (indirect) significant effects on biogeochemical processes (Schmitz et al., 2010), disease (Ostfeld & Holt, 2004; Pongsiri et al., 2009; Braczkowski et al., 2018), invasive alien species (Wallach et al., 2010), and even carbon sequestration (Bressette & Beck et al., 2013). Despite their significance, many of these ecosystem-shaping effects are greatly underappreciated in scientific research (Estes et al., 2011; Somaweera et al., 2020).

In terrestrial ecosystems, many of the largest predators control significant cascading trophic interactions (Ritchie et al., 2012; Ripple et al., 2014). The removal of apex predators increases the pressure of primary consumers on plants, eventually leading to the extinction of some autotrophs (Saint-Béat et al., 2015). The green world hypothesis (GWH), first proposed by Hairston et al. in 1960, contends that predators maintain high levels of global plant biomass by restricting herbivore numbers. Altered states that develop after the loss of apex predators seem to be simpler than the prior state. It supports less biodiversity, suggesting that apex predators play a key role in retaining high biodiversity (Terborgh & Estes, 2010). Apex predators are commonly viewed as the key species in an ecosystem due to the belief that these species exert the most significant influence and are therefore the most vital. However, their role in ecosystems is context-dependent and may vary spatially and temporally (Ritchie et al., 2012). Therefore, it cannot be assumed that apex predators always have the most significant position in a trophic network. For instance, an apex predator species may have a relatively smaller impact within a guild of apex predators (Steinmetz et al., 2013; McPeek, 2014). Although key species are typically predators, they are not always apex predators; instead, they are often secondary consumers (e.g. Paine (1969) and Mills et al. (1993)). Furthermore, herbivores can also play essential roles in ecosystems (Poelman & Kessler, 2016). However, the restoration of apex predators is becoming a growing interest throughout the world as a way to control ecological processes and species abundance for the purpose of biodiversity conservation (Estes et al., 2011).

Although apex predators are considered to play significant roles in an ecosystem, they are among the species most at risk around the world (Terborgh & Estes, 2010). Apex vertebrate predators usually exist at low population densities and have an extensive home range (Ripple et al., 2014). These predators thus rely on habitat connectivity, making them especially susceptible to habitat fragmentation and conversion (De La Torre et al., 2017; Figel et al., 2019). Slow life history makes it so that apex predator populations have a weak response to increased mortality due to the numerous threats the populations face. This is one of the many factors playing a significant role in (anthropogenic-induced) species extinction (Terborgh & Estes, 2010; Ripple et al., 2014). The jaguar (*Panthera onca*), the largest apex predator of the lowland neotropics, serves as a prime representation of these instances (De La Torre et al., 2017; Figel et al., 2019). Currently, the jaguar has been extirpated from over half of its historical range (Sanderson et al., 2002; IUCN, 2017) with their current distribution becoming increasingly fragmented [see Figure 1.1]. As a result, the jaguar is listed as a near-threatened species and the population trend is decreasing in most of its remaining range (Medellín, 2016; IUCN, 2017). The reason

why the jaguar is not listed in a higher risk category, is because the jaguar still exists in a wide geographical range and has a relatively large subpopulation in the Amazon basin. However, the subpopulations are severely fragmented and there is likely very little to no genetic exchange. The vast majority of the remaining subpopulations are considered endangered or critically endangered. The jaguar's status is currently in review and may be elevated to a higher risk category (De La Torre et al., 2017).

Figure 1.1: *The current and former range of apex predator jaguar (Panthera onca) in the neotropics.*

Remark. In the public domain

As a result, there is an increased need to predict jaguar declines and remaining suitable habitats for conservation action. Therefore, much effort has been put into Habitat Suitability Models (HSMs) and Population Viability Analyzes (PVA). These models use environmental variables such as the amount of natural habitat, elevation, distance to rivers, landcover, and human population density, as well as species presence locations, to predict and evaluate the suitability of habitat for species at a given location (Ramirez-Reyes et al., 2016). PVA combines ecological and demographic data with statistics to simulate the dynamics of a population over time. PVA is an important tool in conservation biology for assessing the long-term viability and risk of extinction of populations of endangered or threatened species (Desbiez et al., 2012). By combining habitat suitability and population models, scientists hope to gain a comprehensive understanding of the ecological requirements of apex predators like the jaguar and assess their vulnerability to threats. In the case of jaguars, particular emphasis is being put on conducting these analyses for the remaining patches of the Atlantic Forest, which not only harbor the highest concentration of jaguars but also face significant challenges from widespread deforestation and habitat degradation. Paviolo et al. (2016) is a prime example of a study that shows that by identifying areas of high habitat suitability, researchers can prioritize conservation efforts and target conservation actions where they are most needed.

The jaguar population is experiencing a steady decline, which may lead to the species disappearing from more areas. It has yet to be ascertained what influence this may have on a system, as direct effects of the jaguar's disappearance from its historical range have not been intensively studied due to a lack of perceived need in earlier decades and the difficulty of conducting such research retroactively. Responses of a system usually become evident years later due to the relatively long generation times

species can have (Estes et al., 2011). Anthropogenic factors such as hunting and shifting land uses, as well as natural plant succession, can all have a significant impact and complicate the situation over time. These factors combined, make the effects nearly invisible in local extirpations. Subsequent studies to the responses of local extirpations have therefore lagged for many years (Terborgh & Estes, 2010). So although the jaguar has long been reduced or extirpated from much of their historical range, no direct answer to the effects of their extinction on an ecosystem can be given. Simply because they have not yet been extirpated completely. However, there are documented effects and a lot has been documented about the effects within an ecosystem with the presence of jaguars, which could give valuable insights into the possible effects on a system if these effects were altered. Taking this into account, it is essential to acknowledge that neotropical systems, especially forests, are complex and diverse systems (Estes & Terborgh, 2010; Fayle et al., 2015), and to consider that these factors may act as buffers to prevent (direct) significant impacts or sudden shifts in the trophic network (Morris, 2010). So although the jaguar is an apex predator, it has yet to be ascertained whether its disappearance in this complex system would leave a significant footprint on the ecosystem.

Large carnivores often serve as flagship species for ecosystems worldwide (Ripple et al., 2014). In the lowland neotropics, the jaguar serves as a key species in conservation biology. Recognized as a flagship and umbrella species in this region (Tortato et al., 2017; Mena et al., 2020), the jaguar is considered to play a vital role in maintaining the balance of the ecosystem and the survival of many other species that share its habitat. Conserving the jaguar not only benefits the species itself but also serves as a means of preserving the wider biodiversity. The tendency of umbrella species to have specialized habitat needs across expansive territories is what leads to the broader conservation impact of their protection. Therefore, a protected area that is designed to conserve a vital jaguar population will simultaneously conserve populations of many other co-occurring species in that same area (Thornton et al., 2016). As the prospects for the jaguar are bleak, it is essential to visualize whether or not significant consequences may follow to capitalize on this for conservation.

The purpose of this study is to compile the possible scenarios to better comprehend the potential consequences of the jaguar's extinction as the largest apex predator in lowland neotropical forest ecosystems. It has become evident that human activity cannot substitute for the ecological role of large carnivores in nature (Ripple et al., 2014). These findings are thus crucial for developing successful conservation measures for neotropical forests in the event of a jaguar disappearance, as well as for accurately assessing the potential severity of the problem and strengthening the jaguar's protection to prevent further population reductions. Taking into account the gaps in current knowledge, the following main research question was developed:

What are the possible consequences for ecosystem functioning in the lowland neotropical rainforests if the largest apex predator, the jaguar, became extinct?

The following sub-questions have been formulated to articulate a well-funded answer to this main question:

1. In what ways does the presence and absence of a jaguar influence its prey?
2. How could its disappearance affect other (meso)predators in the same ecosystem?
3. Could another (apex) carnivorous predator take over the jaguar’s place?
4. Which indirect ecological effects on the neotropical forests are likely?
5. How likely is it that the ecological effects could induce a trophic cascade?

Although definitive knowledge of how the absence of a jaguar affects neotropical forests is still actively researched, it is essential to review what is currently known. It is useful to understand the possible (significant) ecological effects of the disappearance of this umbrella species by combining information

and discussing current knowledge in this area. Discussing the results and assessing the severity of the consequences can ultimately be utilized to make decisions on the conservation of the jaguar and the neotropical forest ecosystems it affects and develop more accurate HSMs for conservation measures. It also allows emphasizing the areas that are still greatly understudied and require more in-depth research.

This literature study is meant for those interested in conserving neotropical forests and the ecological role of the apex predator jaguar. It is also meant for those who seek a clear overview of all currently known effects the jaguar has on its environment and what this could mean for the future in terms of the population's ongoing decline. The study highlights the importance of community dynamics and ecosystem health in the neotropics while simultaneously raising awareness about (anthropogenic-induced) apex predator extinction and the effects this could have on ecosystems around us.

2. Methodology

A qualitative systematic literature review was carried out to answer the main question of this study. Using preselected criteria, relevant information was gathered and thoroughly analyzed with the aim to obtain well-supported answers to the sub-questions.

2.1 Used sources

The sources used in this paper are mainly peer-reviewed research papers, articles, books, and literature studies. These sources were obtained from a selection of search engines and databases known for providing peer-reviewed and scientific literature [Table 2.1]. Multiple search engines and databases were used to expand the pool of relevant literature. Alternative information was searched for using Google for general information about the jaguar.

Table 2.1: *Databases and search engines consulted to obtain relevant literature*

Database/search engine	Link
Google Scholar	https://scholar.google.com
Wiley	https://onlinelibrary.wiley.com
WUR Library	https://wur.on.worldcat.org/discovery
ScienceDirect	https://www.sciencedirect.com
ResearchGate	https://www.researchgate.net
Springer Link	https://link.springer.com

2.2 Keywords and citation searches

Relevant literature was searched for using certain combinations of keywords. The keywords were combined in search engines using 'AND' or 'OR' to find the most relevant literature for the sub-questions. For more detailed information, double quotations ("…") were used to ensure the involvement of specific information needed to answer sub-questions. Table 2.2 shows the most-used keywords per sub-question of this study.

Table 2.2: *Used keywords to find relevant literature per sub-question*

Sub-question	Keywords
In what ways does the presence and absence of a jaguar influence its prey?	Ecological effects, ecosystem, jaguar, neotropics, forest, prey, behavior, absence, presence, influence, opportunist, habitat, distribution, effect, negative, positive, panthera onca, population, species, communities, *name of prey species*
Which indirect ecological effects on the neotropical forests are likely?	Indirect, effects, ecosystem, neotropics, ecological, ecology, jaguar, panthera onca, influence, forest regeneration, habitat, disease, carbon, invasive species, forest
How could its disappearance affect other (meso)predators in the same ecosystem?	Mesopredator, jaguar, *name of (meso)predator*, behavior, distribution, neotropics, sympatric, population, effect, disappearance, effect, influence, species, community structure
Could another (apex) carnivorous predator take over its place?	Jaguar, ecosystem, neotropics, panthera onca, change, substitute, take over, effects, distribution, population, effects, influence, *name of carnivorous (apex) predator*
How likely is it that the ecological effects could induce a trophic cascade?	Jaguar, trophic, cascade, influence, ecosystem, prey, top-down, bottom-up, neotropics, forest, pressure, effect, negative, positive, panthera onca, function, threats, influence, population dynamics

Both forward- and backward citation searches were conducted in addition to the keyword searches. Forward- and backward citation searches help to assess the significance and relevance of a study and are useful in discovering other relevant papers cited in the study. The backward citation searches also help to identify the source of certain information and evaluate its relevance in the present. Additionally, both forward- and backward citation searches can provide new insights and reveal more relevant keywords, thereby expanding the scope of available literature.

2.3 Literature criteria and reliability

To ensure the reliance and relevance of the used literature, the papers must meet predefined criteria [Table 2.3]. Papers not meeting the criteria are excluded from this literature study.

Table 2.3: *The criteria for inclusion and exclusion of literature used for this study*

Included literature	Excluded literature
Non-recent literature providing data still applicable to present-day discoveries.	Non-recent literature contradictory to recent discoveries.
Peer-reviewed literature and non-peer-reviewed literature stating information that aligns with the information in peer-reviewed literature.	Non-peer-reviewed literature contradictory to peer-reviewed literature.
Literature used to answer questions about the specific ecological effects of jaguar must apply to neotropical forests.	Articles about ecological effects on other neotropical habitats e.g. wetlands, scrublands, deserts, river valleys, grasslands, and agricultural land (including cattle) are excluded.
Unbiased literature based on factual evidence.	Literature based on the author's opinions, beliefs, or prejudices.

The relevance of a source was initially determined by examining the publication date and conducting a forward citation search, followed by a review of the paper's title and abstract. As this paper has a focus on the effects of the disappearance of a species from a system, it is linked to historical data as the jaguar's decline has been going on for many decades. Historical data may therefore offer valuable historical perspectives, which can provide a deeper understanding of this particular research area. Including older publications can enrich the analysis and interpretation of current findings, and contribute to a more comprehensive understanding of the field. Older papers are thus not excluded from this study. However, these older papers will only be included if they add valuable information and are not contradictory to recent discoveries. Using both recent and older publications will provide the most useful data and the best-informed answers and insights based on current available information.

Language searches

This paper will not impose language-based restrictions. Although the search will prioritize English literature, papers in other languages (e.g. Spanish, Portuguese, and French) that are frequently cited by relevant English papers will also be included. These non-English papers will be translated using the DeepL Translator. Notably, Spanish and Portuguese are the predominant languages spoken in neotropical regions. Any exclusion based on language may lead to the omission of crucial information, discoveries, and findings, which is why they are included.

2.4 Literature review and analysis

This study employs a dual-analytical approach in conducting the literature review, using both a within-study analysis and a cross-study analysis. The cross-study analysis was used to comparatively assess individual sources and obtain insights into potential disparities in the information contained within.

The within-study analysis was used to thoroughly examine individual sources and extract relevant information of significance. Both analytical methods were employed throughout the research process to ensure an adequate comparison and evaluation of the findings while taking into account the content of relevant literature.

Given that this study is a qualitative systematic literature review, it utilizes an interpretive approach to analyze textual data and identify key themes, patterns, and connections among the relevant literature. This approach was applied to each sub-question in which all criteria-meeting literature was analyzed and the relevant data synthesized. During this process, different perspectives in the data were highlighted to allow for nuanced answers to the sub-questions. The results section presents the analyzed and synthesized information in a structured manner per sub-question, providing a comprehensive overview of the findings in a quantitative manner.

3. Results

The examination of apex predator decline or extinction in ecosystems presents a rare but valuable opportunity to understand how the ecological context of an ecosystem influences the strength of predator effects on ecosystem structure and function (Ritchie et al., 2012). Roaming the dense rainforests of the Americas, the jaguar embodies an apex predator that holds a great influence over its surrounding ecosystem. The jaguar's influence radiates through multiple levels, making it important to research these levels as thoroughly as possible to obtain a complete picture. This chapter summarizes the available relevant information about the influences of the (absence of the) jaguar on neotropical forest ecosystems. The jaguar's interactions with its prey and other predators, potential niche takeovers, indirect effects on ecosystems, and possible cascading effects are discussed, examining the intricate web of relationships and the profound impacts they have on these ecological factors. To fully comprehend the effects of a jaguar's disappearance on an ecosystem, it is necessary to first understand their influence when they are present within that ecosystem. Following this, the potential outcomes and scenarios that could arise in the absence of jaguars from the ecosystem are examined and summarized following the order of the sub-questions.

3.1 In what ways does the presence and absence of a jaguar influence its prey?

Understanding the intricate relationships between predators and their prey is crucial for comprehending the dynamics of ecosystems. In this chapter, the influences exerted by jaguars on their prey species are explored. By investigating the ecological interactions, hunting strategies, and population dynamics involved, the profound impacts jaguars have on the abundance, behavior, and distribution of their prey will be clarified.

3.1.1 The jaguar's prey

The first crucial factor to note is that the jaguar's occurrence, along with other predators, is primarily influenced by the abundance of prey, rather than the other way around. The essential role of prey in shaping the presence and distribution of large predators within an ecosystem has therefore been well-established in recent ecological research. The feeding ecology of such predators is intricately tied to the availability and relative abundance of prey species. In the case of jaguars, which tend to largely exhibit an opportunistic hunting strategy, their prey selection is primarily influenced by chance encounters with locally available prey, especially in rainforests. (Sunquist & Sunquist, 2002)

To understand how the jaguar's presence and absence affect its prey, it is essential to determine the particular species that the jaguar preys upon. Various studies of jaguar scat have shown that their diet consists predominantly of terrestrial mammalian species, with (aquatic) avian and reptilian prey being less frequently consumed (Emmons, 1987; Aranda & Sánchez-Cordero, 1996; Taber et al., 1997; Weckel et al., 2006). Hayward et al. (2016) conducted a thorough literature review to investigate the main dietary preferences of jaguars. The study found that, although jaguars are opportunistic feeders, they exhibit selective feeding habits based on certain characteristics of their prey, which renders the term "opportunistic" slightly inaccurate. The authors reported that jaguars tend to prefer capybaras and giant anteaters when they are available prey species but avoid species that do not fall within their accessible and preferred weight ranges such as adult tapir, as they typically target prey slightly smaller than themselves. However, socio-ecological factors such as prey abundance and behavioral traits, such as herd size, appear to play a more significant role in shaping jaguar foraging decisions rather than morphological traits such as body size, which is likely the reason they also tend to avoid agoutis and carnivorans. The avoidance of species typically occurs when there are other “better” available options. This shows a tendency of jaguars to make foraging decisions based on cost-effectiveness. Nevertheless, the particular prey preferences of jaguars may vary depending on factors such as the specific region

and the availability of prey. However, it is important to note that the prey preferences are not the same as the most frequently consumed prey species, as this is highly dependent on population sizes and regional occurrence. Some species have a bigger population size, increasing the encounter rates.

Based on numerous studies, peccaries consistently emerge as a primary component of the jaguar's scats and diet, though regional variation still plays an important role in prey preference. For instance, Aranda & Sánchez-Cordero's publication in 1996 showed that white-lipped peccaries were frequently found in jaguar scats in Costa Rica, Emmons' study in 1987 in Cocha Cashu, the Peruvian Amazon, showed that collared peccaries and agoutis were most preferred. In Belize, the preferred prey species appeared to be mostly collared peccaries, pacas, and nine-banded armadillos according to Weckel et al. in 2006. Jaguar seems to avoid tapir in both the Peruvian Amazon and Belize and white-lipped peccaries were commonly consumed in Costa Rica but they were not commonly found in scats in Belize, further demonstrating the regional varieties in preferences likely based on prey availability. Although the preferred prey species varies per region, white-lipped peccaries, collared peccaries, capybaras, giant anteaters, white-nosed coatis, and nine-banded armadillos are generally the most frequently consumed prey species by jaguars (Emmons, 1987; Foster et al., 2010; Hayward et al., 2016).

3.1.2 Impacts on prey species and populations

To further investigate the impacts of jaguars on their prey species, a few studies will be brought forward that demonstrate certain impacts of its presence in the system and what this could mean if the effects were altered. The absence of apex predators is generally associated with an increase in prey abundance due to predation release (Terborgh et al., 2001; Estes & Terborgh, 2010; Ripple et al., 2014; Ripple et al., 2016). However, the significance of the jaguar's impact on a specific prey species' population is likely to differ. The low population density of giant anteaters, for example, may lead to a higher impact on these populations in comparison with capybaras or white-lipped peccaries with higher population densities. Giant anteaters are solitary territorial animals and capybaras and white-lipped peccaries live in groups or big herds (Kiltie & Terborgh, 1983; Herrera et al., 2011). Capybaras and white-lipped peccaries also have a higher reproduction rate in comparison with giant anteaters, who only give birth to one young a year (Desbiez et al., 2020). The jaguar's influence on giant anteater is quite significant as the encounter rates greatly increase in the absence of the jaguar (Quiroga et al., 2016). However, giant anteaters are typically eaten in proportion to their abundance (Cavalcanti & Gese, 2010) whereas several studies have demonstrated that jaguars can have a significant impact on peccary populations. As mentioned, peccaries typically tend to be the primary component of the jaguar's diet in various regions. In Corcovado National Park in Costa Rica, white-lipped peccaries are a major prey species for jaguars, with 89% of scat samples containing evidence of their consumption (Carillo et al., 2009). Similarly, in Sierra Madre de Chiapas in Mexico, jaguars were found to kill collared peccaries at a much higher rate than other prey species (Cruz et al., 2007), and in Iguaçu National Park in Brazil, jaguars were found to be responsible for killing about half of the peccary population annually (Crawshaw, 1995).

In contrast, however, Wright et al. (1994) carried out an experiment in two neotropical forests revealing that the absence of apex predators jaguar and puma may not always be the primary cause of population growth or decline of large herbivorous mammals. The study contrasted Cocha Cashu (Peru), where jaguars and pumas were still present, with Barro Colorado (Panama), where they had been extirpated. It was found that mammal densities generally did not systematically differ between the two sites. This observation gave rise to three potential hypotheses: (1) that there was no interaction between apex felid densities and prey densities, indicating that the top-down effect was not controlled by the large felids; (2) that the effects were masked through anthropogenic factors such as hunting and poaching; or (3) that the effects were inconsistent due to the opportunistic diets of the

two species. Emmons (1987) and Wright et al. (1994) reported that Dasyprocta (agoutis) exhibited the highest population densities in the absence of apex predators, thereby suggesting that apex predators, such as jaguars, could influence prey densities. However, it does not imply that prey is all or always limited by predation as food resources are also a limitation to population growth (Emmons, 1987).

As the above studies reflect, the interplay between predators and their prey is a complex ecological process wherein prey species can initially shape the presence and distribution of predators, but subsequently, once predators have become established, they can significantly impact the dynamics of their prey populations as well. In recent years, it has become increasingly apparent that the impact of predators on prey extends beyond the direct killing of individuals. This has given rise to the concept of "the ecology of fear", which was first proposed by Brown et al. in 1999. The ecology of fear refers to the behavioral responses of prey animals to the perceived risk of predation, driven by fear. The induced behavioral changes in prey can be ecologically significant when jaguars are present. The increased stress and fear responses can have significant effects on the prey's resource intake, metabolic utilization of nutrients, and reproduction (Letnic & Dworjanyn, 2011). Furthermore, it is also known to cause alteration in foraging patterns and habitat utilization of prey species by avoiding high-risk areas and spending more time in areas with low predator densities (Oriol-Cotterill et al., 2015). These fear-induced responses have been found in capybaras. Avila et al. (2022) demonstrated that capybaras spend more time foraging in safe areas such as riversides and show increased herding behavior when they face regular jaguar predation. Capybaras occurring in predator-free areas did not show this behavior as they do not recognize predator (sound) stimuli. The same behavioral changes have been found in peccaries, especially white-lipped peccaries (Kiltie, 1980). However, white-lipped peccaries have also been found to be capable of mobbing jaguars, showing aggressive behavior, and causing jaguars to flee (Rampim et al., 2020).

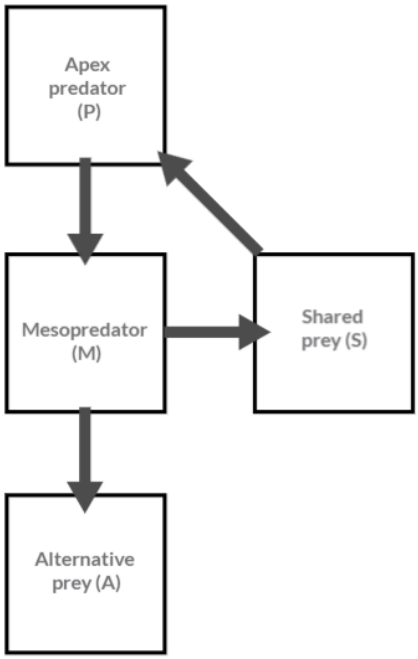
These instances indicate that jaguars have the tendency to shape behavior, distribution, and abundance of prey (Terborgh et al., 2001) but their influence is dependent on forage decisions which are shaped by the socio-ecological characteristics of prey. As has become apparent by these studies, the response of a prey species to predator extirpation is influenced by its unique life history and ecological characteristics. Consequently, changes in the composition of ecological communities resulting from predator extirpation can follow multiple pathways depending on these factors (Fahrig, 2017; Pires & Galetti, 2023) though not all are fully understood. The impacts on prey and prey populations are direct but can lead to follow-up indirect consequences, which will be discussed further in chapter 3.4.

3.2 How could its disappearance affect other (meso)predators in the same ecosystem?

Jaguars, among other apex predators, possess the ecological capacity for top-down influences of mesocarnivore populations and thereby likely disrupting predator-prey interactions (Galetti et al., 2013). This influencing capacity stems from a diverse array of mechanisms, which may involve direct predation, competition for shared resources, and inducing changes in prey behavior that limit population growth rates (Ritchie & Johnson, 2009; Ripple et al., 2014; Prugh & Sivy, 2020), However, they can also serve as an ecological subsidy for mesocarnivores by supplying carrion as a food source (Emmons, 1987; Moleón et al., 2014; Escobar-Lasso et al., 2016).

The removal of an apex predator like the jaguar from an ecosystem can lead to mesopredator release and increased activity levels (Roemer et al., 2009), which may, in turn, contribute to a decline in prey populations. However, this relationship is complex, highly context-dependent and influenced by two critical factors: the productivity of the ecosystem and the strength of interactions among apex predators, mesopredators, and prey within that ecosystem as illustrated in Figure 3.1. In areas with limited prey abundance, mesopredators may not be regulated by predation but rather by the scarcity of their food source. On the other hand, in areas with abundant food supply, mesopredator populations are likely to increase once control by apex predators is removed as the absence of apex predators can simultaneously lead to an increase in prey (Nishijima et al., 2014; Ripple et al., 2016). The degree of mesopredator release is expected to be most significant in systems with strong links between species. In this regard, high species diversity and a wide range of diet niche breadths are factors that could reduce the intensity of mesopredator release. The effect of apex predator removal is likely to be less pronounced in systems with many apex predators, mesopredators, and prey species than in those dominated by only a few species (Brashares et al., 2010) which would result in a dampening of effects in complex tropical ecosystems. In the absence of apex predators, it is most likely that mesopredator density is predominantly bottom-up controlled by prey densities (Ritchie & Johnson, 2009).

Figure 3.1: *Interactions between apex predators (P), mesopredators (M), and available prey (A, S).*



Remark. Adapted from "Roles of alternative prey for mesopredators on trophic cascades in intraguild predation systems: a theoretical perspective" by Nishijima et al., 2014, *The American Naturalist*, *183(5)*, p. 625-637. Copyright 2014, Nishijima et al.

Looking at specific predator species, the jaguar seems to have a less significant impact on ocelots as ocelots do not seem to avoid jaguars in areas they live in sympatry (Emmons, 1987). In the Atlantic Forest of Brazil, this instance has been demonstrated to be true. In a study conducted by Massara et al. in 2016, it was hypothesized that the presence of large felids such as jaguars and pumas may limit ocelot abundance. However, in this study and other recent studies, it has been shown that ocelots seemed more abundant in areas inhabited by both felids as long as the areas were relatively large and well-protected (Di Bitetti et al. 2010; Massara et al. 2015). Though the ocelot's presence may not be much affected, Massara et al. (2016) also showed that other smaller cats such as jaguarundi and oncilla do seem to be species that negatively correlate with the presence of jaguar, which may be the result of fear (Brook et al., 2012; Prugh & Sivy, 2020). This indicates that the absence of the jaguar may have a positive effect on these species' occurrences.

Jaguars also seem to impact (meso)predators in other ways. Jaguars are predominantly nocturnal predators and in the Misiones region of Argentina it was shown that pumas tend to become more nocturnal in areas where jaguars are less abundant (Paviolo et al., 2009), showing the potential for jaguars to alter the behavioral patterns of other predator species, in this case, hunting strategy. Some studies also suggest that pumas may be excluded by jaguars through competition. Furthermore, dietary shifts have been confirmed in ocelots and pumas in the event of a jaguar decline which causes prey shifts. In comparison to sights where the jaguar was present, ocelots shifted to more medium-sized prey whereas they usually prefer smaller prey (Emmons, 1987; Moreno et al., 2006) and puma shifted to a diet containing more peccaries (mostly collared peccaries) than deer. It has been suggested that this may be the result of a combination of these predators expanding their niche due to the events of competitive release and an increase in the prey species such as the peccaries due to predation release from jaguar (Moreno et al., 2006).

3.3 Could another (apex) carnivorous predator take over the jaguar's place?

In the neotropical forest ecosystems, there are two predators considered the apex predators of this region. These are the jaguar as the largest apex predator of the neotropics and the similar-sized but second-largest, puma (*Puma concolor*), occurring sympatric with jaguars (Foster et al., 2010). It is therefore the closest predator to the jaguar that could potentially play a role as surrogate species. The two felids have a significant overlap in their distribution across the neotropics. In areas the species co-occur, the felids tend to show mutual avoidance. This was demonstrated by Emmons (1987), who observed that when both species are hunting simultaneously, they do so in distinct territories. Also in large spatial contexts, pumas seem to be rare in areas with high jaguar abundance (Azevedo & Murray et al., 2007). However, studies such as that of Harmsen et al. (2009) show that activity patterns are similar between the two species.

In tropical forests, strong vertical links between predator and prey populations are scarce. The closest link that can be found in the neotropics is the link between the jaguar and the prey species capybara and peccaries (Emmons, 1987). The question remains, however, whether puma would turn to these species as major prey species in the absence of the jaguar (Terborgh & Estes, 2010). Although both felids are opportunistic feeders, puma more so than jaguar as they also consume smaller prey (Sollmann et al., 2012), their diet does not completely overlap (De Azevedo, 2008; Di Bitetti et al., 2010). Taber et al. (1997) showed that the jaguar mainly takes more large prey than puma in untouched areas such as forests and has an overall diet overlap of 65%. Recently, it has also been found that pumas, are not strongly associated with white-lipped peccaries (Flores-Turdera et al. 2021), while jaguars heavily rely on this species in certain regions (Carrillo et al., 2009; Flores-Turdera et al. 2021). Pumas typically feed more on deer (red brocket deer) in co-occurring areas with jaguars (Aranda & Sánchez-Cordero, 1996; Sunquist & Sunquist, 2002) but capybara as well as giant anteaters, species frequently appearing in the jaguar's diet, do not appear often in a puma's diet.

One of the main reasons for the differences in diets has to do with the distinct physical characteristics of the two felids. The local food habits of jaguars cannot be attributed solely to the availability of prey in a specific area. This is because jaguars have a robust physique and a large head, which allows them to hunt and kill larger and more heavily armored animals such as giant anteaters and armadillos than pumas can (Emmons, 1987; Aranda & Sánchez-Cordero, 1996; Harmsen et al., 2010) [see Figure 3.2]. Due to their robust build, jaguars likely kill a greater amount of prey than pumas as jaguar scats are often overrepresented (Emmons, 1987). Relative to body size, jaguars also appear to possess proportionally larger and more robust canine teeth than those found in other felid species (Meachen-Samuels & Van Valkenburgh, 2009). In areas the species live in sympatry, jaguars are likely to be competitively dominant over pumas due to these physical characteristics (Sollmann et al., 2012). This further demonstrates the earlier-mentioned potential of dietary shifts and niche expansion in the events of competitive release, as was described by Emmons (1987) and Moreno et al. (2006).

Figure 3.2: *A side-by-side image comparing a jaguar and a puma, showing the jaguar's robust physique and larger head in contrast to the puma.*

Remark. Left: Brian Mckay, 2009. CC BY 2.0. Right: in the public domain.

It is possible for jaguars and pumas to coexist as they avoid direct competition, have different hunting strategies, and have slightly different prey preferences (Aranda & Sánchez-Cordero, 1996). Although full compensation does not seem likely, the potential for dietary shifts and niche expansion in pumas shows a potential for partial surrogation by puma in the absence of a jaguar. A beneficial characteristic of pumas is that they are greater generalists and more tolerant to anthropogenic landscape alterations in comparison to jaguars (Sollmann et al., 2012). Co-occurring mesocarnivores are not likely to surrogate for jaguars or any apex predator as they have weaker effects and different characteristics and diets which do not allow for substitution (Avrin et al., 2023).

3.4 Which indirect ecological effects on the neotropical forests are likely?

Indirect effects of predators can be challenging to foresee due to the complexity of an ecosystem with its great diversity of different pathways and many trophic levels that can potentially be affected by them (Ritchie & Johnson, 2009). However, several studies have shown apparent indirect effects the jaguar has on neotropical forests or apex predators have on ecosystems in general. Most indirect effects flow through the impact jaguars have on their prey and co-occurring mesopredators. Predator loss in an ecosystem can influence various functions such as forest composition and seed recruitment, alteration in prey behavior, nutrient cycling, the release of invasive and exotic species, and disease regulation (Estes et al., 2011; Ripple et al., 2014).

3.4.1 Forest composition and seed recruitment

To investigate the impacts of jaguars in terms of indirect ecological impacts, it is important to consider that most of the prey species are seed predators and seed dispersers. It has been well established that seed predators and seed dispersers have a great influence on shaping forest composition and seed recruitment. In the absence of these species, there is a tendency for large seeds of tree species to accumulate under parent trees, resulting in either monotypic forest patches or seedling mortality (Beck et al., 2013). Seeds may also get trapped in the soil through trampling and soil compaction, making it unable for them to sprout when they are not brought up by the foraging behavior of, for example, peccaries (Villar et al., 2020). The absence of jaguars from the neotropical forest ecosystems is thus most likely to result in indirectly having significant impacts on the patterns of seed dispersal, herbivory, and plant recruitment.

In 1988, Terborgh put forward that larger vertebrate seed predators, which preferentially target tree species with large seeds, are normally kept in check by apex predators such as jaguars. The presence of jaguars promotes seed recruitment of these large-seeded tree species. However, if jaguars were to disappear from the ecosystem, the forest composition could shift over time as larger-seeded tree species may be more vulnerable to predation by seed predators, resulting in a shift towards smaller-seeded species. This could ultimately cause indirect effects on other species within the community. A decade later, Terborgh et al. (2001) conducted a study that demonstrated how the absence of apex predators can impact the structure and diversity of vegetation. The research showed that locations without jaguars, and therefore lacking a full complement of neotropical predators, had higher densities of herbivore prey species and lower densities of saplings than sites where neotropical predators were present in their entirety. They indicated that the densities of seedlings and saplings of canopy trees are severely reduced by herbivores in the absence of top-down regulation. However, the authors noted that this scenario is likely to be transient until the species composition of vegetation adjusts to impose regulation from the bottom up. Terborgh and Wright (1994) carried out an experiment in reverse that showed a similar outcome when looking at the effects of herbivory on plant recruitment. In their experiment, large herbivorous mammals were deliberately excluded from two neotropical forests, namely Barro Colorado in Panama and Cocha Cashu in Peru. The results indicated a significant increase in survival rates and abundance of seedlings and understory herbs when these mammals were absent, further demonstrating the pressing effects of herbivore species on plants.

Two species appearing in the jaguar's diet, seem to have the most significant effects on their environment. White-lipped peccaries (*Tayassu pecari*), a frequently consumed prey species by jaguars in the neotropical forest ecosystem, hold the distinction of being the largest seed predators, mostly large and hard palm nuts, and contribute significantly to the vertebrate biomass of the region (Kiltie & Terborgh, 1983; Jorge et al., 2013). With herd sizes reaching up to 300 individuals and in some instances even 1000 individuals (Kiltie & Terborgh, 1983), the species is known to clear and redistribute litter, root soil, and create and maintain wallows (Beck et al., 2010). As a result, they are considered

ecosystem engineers and play a key role in shaping the food webs within the neotropical forests (Jorge et al., 2013). The second species are the tapirs (*Tapirus]*. Although tapirs are not among the most preferred prey species of jaguar and avoidance is shown in the availability of other prey species, there are areas in which it is considered an important part of its dietary breadth (Emmons, 1987). It is therefore important to mention this prey species since tapirs are the largest herbivore in the neotropics and play a fundamental role in the long-distance seed dispersal of many large-seeded species as well as the predation of seedlings. Its role also does not overlap with other seed dispersers or seedling predators, meaning its role in the system is unique (Jorge et al., 2013). Their long-distance seed dispersal plays an important role as it has been established that this characteristic of tapirs can be crucial in the connection of plant populations in fragmented forested areas (Paolucci et al., 2019). An alteration in behavior or population sizes of these prey species could potentially have significant indirect effects on alterations in forest composition, seed recruitment of large-seeded species, and habitat connectivity for plants in the events of predation release within the regions where they are preyed upon by jaguars.

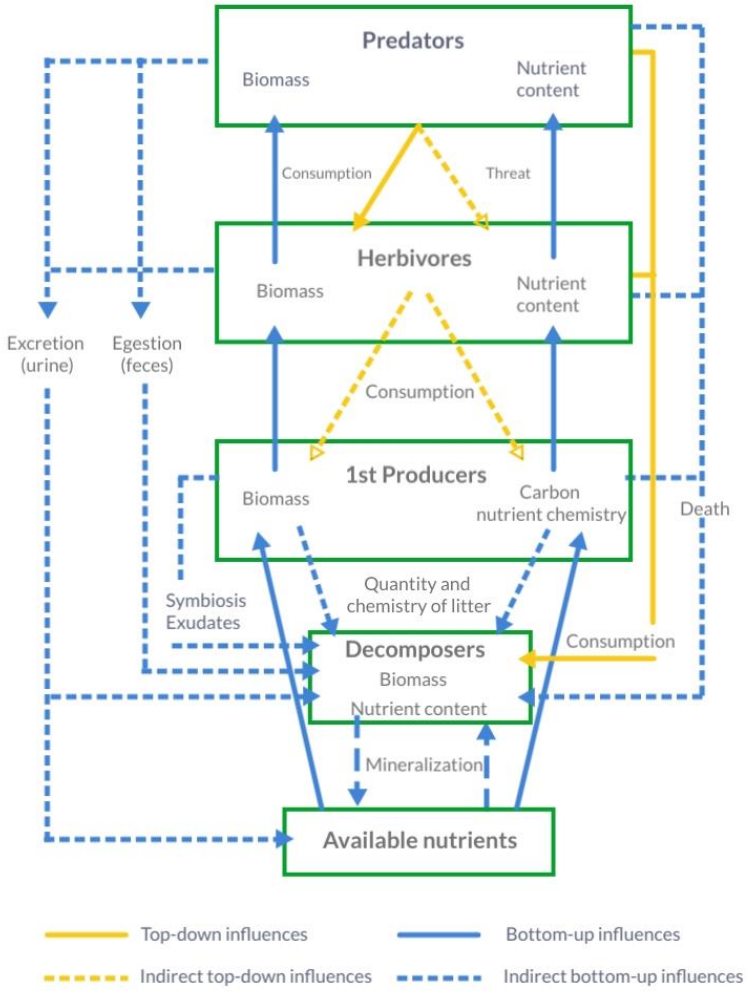
3.4.2 Prey behavior

As the ecology of fear describes, the behavioral changes in prey species can lead to the alteration in foraging patterns and habitat utilization of prey species by avoiding high-risk areas and spending more time in areas with low predator densities (Brown et al., 1999; Oriol-Cotterill et al., 2015). The extirpation of jaguars can alter these patterns which can indirectly lead to changes in forest compositions. As a result, they help regulate the distribution and behavior of their prey species, which can indirectly influence vegetation patterns and modify the structure of the ecosystem. For instance, jaguars may limit the movement of prey into certain areas or prevent excessive browsing, allowing vegetation in those regions to recover (Terborgh et al., 2001). The herding behavior of the main prey species white-lipped peccaries, for example, is beneficial as a defense mechanism as well as improved foraging (Kiltie & Terborgh, 1983). Bigger herd sizes have a greater impact on forest composition rather than smaller herd sizes. The absence of jaguars leads to the predation release of white-lipped peccaries as they will be preyed upon less, given that they are not known to appear often in other predators' diets (Flores-Turdera et al. 2021). Changes in herd sizes, such as them becoming smaller in the events of predation release, might ultimately lead to these effects within the forest ecosystems.

3.4.3 Nutrient cycling

Nutrient cycling is often associated with strong bottom-up forces. However, nutrient cycling in ecosystems not only depends on bottom-up forces but also on top-down forces. Figure 3.3 shows a framework of the nutrient dynamics in the trophic ladder. Through recent years it has become more apparent that apex predators seem to have a great influence on nutrient cycling, though mostly indirectly. In a study by Schmitz et al. (2010), researchers investigated the mechanisms through which predators influence nutrient dynamics within an ecosystem. Consumptive effects entail the direct transfer of energy and matter as prey is digested, and nutrients are subsequently stored, translocated, and released into the environment. Non-consumptive impacts, on the other hand, are indirect and originate from prey's triggered responses to predator presence. These responses are associated with the prey's "ecology of fear" (Brown et al., 1999) and manifest themselves in three ways: habitat shifts aimed at seeking refuge from predators, stress-induced changes in metabolic nutrient utilization, leading to changes in the intake and release of specific nutrients, and dietary adjustments that balance the trade-offs between risk avoidance and foraging. Pointing out the specific indirect effects jaguars may have on nutrient cycling is challenging as non-consumptive effects are not easily visible in complex systems. Predator exclusion in experiments is therefore required to be able to comprehend these effects.

Figure 3.3: Conceptual framework of the *nutrient dynamics in the trophic ladder showing that predators also influence nutrient cycling.*



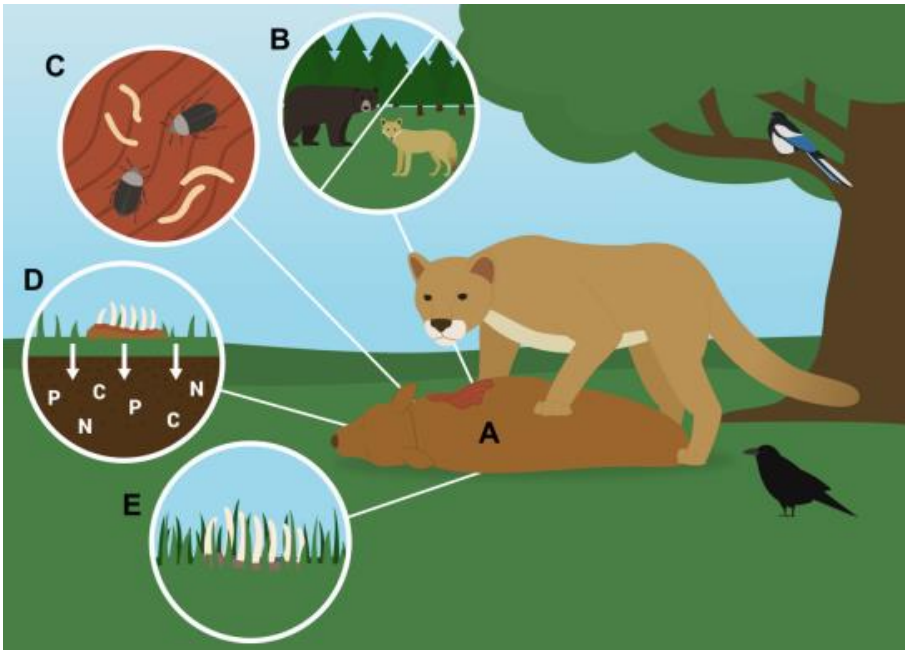
Remark. Adapted from *Trophic Ecology* (p. 234) by S.E. Hobbie and S. Villéger, 2015, Cambridge University Press. Copyright 2015, Cambridge University Press.

The absence of jaguars is expected to have a significant impact on nutrient dynamics by influencing the alteration of prey species' habitat usage and overall distribution in an area. When predation pressure is released, it often leads to changes in prey habitat selection, resulting in increased grazing and foraging pressure at specific sites. Prey species typically prefer areas with high primary productivity but may avoid these regions in the presence of predators, creating a trade-off between risk avoidance and foraging. An example from Yellowstone National Park, where wolves were absent, demonstrated that ungulates heavily grazed on productive grasslands. However, the reintroduction of wolves resulted in a substantial reduction in grazing impact at these sites, leading to a 50-60% decrease in nitrogen (N) mineralization rates and the consumption of N, phosphorus (P), and other macronutrients. Similarly, jaguars may indirectly affect nutrient cycling by primarily altering mineralization rates, causing either an increase or decrease, thereby changing the carbon-to-nitrogen-to-phosphorus (C:N:P) ratios and nutrient intake (Schmitz et al., 2010). This could also impact the nutrient quality of resource tissues, which are eventually released as detritus into the dead organic matter pool, consequently influencing decomposition rates. An experiment conducted by Dunham (2008)

demonstrated that vertebrate predators in tropical forests enhance inorganic phosphorus (P) levels in the soil through this indirect pathway.

An additional pathway that can significantly impact nutrient dynamics within an ecosystem is through the distribution of carcasses and carrion [Figure 3.4]. Jaguars often leave a substantial portion of their large prey species unconsumed after a kill (Emmons, 1987). This facilitates mesocarnivores with resource subsidies (Meleón et al., 2014; Pereira et al., 2014; Johnson-Bice et al., 2023). Furthermore, the presence of unconsumed prey carcasses can result in the formation of nutrient hotspots within the ecosystem (Schmitz et al., 2010; Johnson-Bice et al., 2023). When these carcasses become part of the detritus pool, they contribute a concentrated source of nutrients to specific areas. These nutrient-rich patches typically emerge in high-risk areas or refuge spots of prey species as well as in the feeding areas utilized by the jaguars. The detritus from these unconsumed prey carcasses acts as a localized source of nutrients, which can have effects on nutrient cycling and primary productivity. (Schmitz et al., 2010). By leaving unconsumed portions of their kills, jaguars indirectly contribute to the redistribution and concentration of nutrients within the ecosystem. This phenomenon has implications not only for the scavenging mesocarnivores but also for the nutrient availability and utilization by other organisms within the ecosystem. Through this pathway, the absence of a jaguar could indirectly reduce the occurrence of nutrient hotspots, leading to a decrease in the availability of high-productivity areas and nutrient redistribution. Consequently, this has an effect on mineralization and decomposition rates in these areas.

Figure 3.4: *Schematic image showing indirect effects of predators leaving a carcass.*



Remark. When the predator in a system kills a prey (A), mesopredators and scavengers respond to the carcass site (B) leading to interspecific interactions. Unique arthropod communities develop to decompose organic matter (C). With the decomposition of the carcass, C, N, and P leach into the soil (D). This in turn increases productivity in this through increased soil nutrients, enhancing plant growth (E). Figure adapted from *Patchy indirect effects: predators contribute to landscape heterogeneity and ecosystem function via localized pathways* by Johnson-Bice et al., 2023, University of Minnesota. Copyright 2023, University of Minnesota.

3.4.4 Release of invasive and exotic species

The extirpation of apex predators releases prey from predation pressure, which may not only allow for the increase of native prey species but also of exotic and invasive prey species populations (Pellerin et al., 2006). An example of an exotic and invasive species in the neotropics is the introduced and invasive wild boar (*Sus scrofa*). This species is one of the most widespread and destructive terrestrial mammals and has been expanding in Brazil's Atlantic Forest (Pedrosa et al., 2021). Wild boar act as effective seed dispersers and also promote long-distance seed dispersal of zoochorous plants in these areas. This could have positive effects on the ecosystem as they could substitute for the role of tapir in regions that are widely defaunated such as the Atlantic Forest (Paviolo et al., 2016; Pedrosa et al., 2019; Pedrosa et al., 2021). However, their capacity to easily adapt (also to increased fragmenting landscapes) and expand may also lead to the dispersion of exotic and invasive plant species, facilitating changes in the structure of natural forest ecosystems. These plant species usually originate from agricultural areas in which the plant species have been introduced as livestock forage (Pedrosa et al., 2019; Pedrosa et al., 2021).

Wild boar act as an alternative prey species to the jaguar in regions their distributions overlap and they have been found to appear in the jaguar's diet (Cavalcanti & Gese, 2010). Adult wild boars are too big in body size in relation to jaguars so they are likely to prey upon juveniles and piglets. Jaguars alone are not capable of keeping wild boars under control, especially not given their high reproductive rates. However, their combined impact with pumas may be able to facilitate this as pumas have also been proven to consume wild boar (Hegel & Marini, 2018). However, with the decline and disappearance of jaguars in the Atlantic Forest, there is a lack of full apex predator complement, leaving wild boars without a strong enough predation pressure, allowing them to keep expanding their population (Pedrosa et al., 2021). Although a full complement of predators would influence wild boar, the question remains whether this would be significant.

3.4.5 Disease regulation

The role of predators in disease transmissions has been of growing interest in recent studies. The transmission of diseases tends to increase when host prey populations are densely concentrated, particularly in cases where the hosts gather in herds, such as peccaries. However, the presence of predators can mitigate the spread of disease within populations by preying on the hosts. Predators often exhibit a preference for hunting infected prey, as they are typically weaker and easier to capture (Hatcher et al., 2006). By preying on infected hosts, predators could reduce host densities, thereby inhibiting the spread of the disease. Nevertheless, the success of this disease control mechanism relies on the conditions that the predators do not further spread the parasites themselves when they consume infected prey. If this condition is met, removing infected prey from populations prevents further spread of the parasites. Consequently, contact between susceptible and infected host species diminishes, hindering the transmission of the disease (Duffy et al., 2011).

Predators could thus reduce disease prevalence in prey populations by removing infected hosts and thereby reducing host density in herds (Duffy et al., 2011). Diminishing host densities and preying upon infected hosts can drive a parasite to extinction if the population size threshold is not met. This is a result of the requirement of invading parasites for a minimum host population size for invasion and a minimum propagation size of infected individuals. Predators have the influencing capacity to keep those numbers below the critical point. Removal of the jaguar from a system could in theory elevate disease in host prey species. This especially occurs in the events of cumulative effects such as the selection of predators for infected hosts, hosts being infected with a highly virulent parasite, and the hosts having a long lifecycle, further increasing the likelihood of disease spread (Packer et al., 2003). This could have the most significant impact on the jaguar's prey species which are typically less preferred by other predator species in neotropical forest ecosystems, such as white-lipped peccaries.

However, it must be considered that prey form bigger herds in the occurrence of jaguar predation, which might be a factor contributing to the elevation of disease spread in these herds.

3.5 How likely is it that the ecological effects could induce a trophic cascade?

Ripple et al. (2016) defined a trophic cascade as "*indirect species interactions that originate with predators and spread downward through food webs*". They specifically mention that bottom-up forces should not be viewed as a trophic cascade as they view trophic cascades are usually driven by consumptive effects. However, the effects that apex predators have in a system go beyond a simple top-down predator-prey interaction. It is greatly dependent on the context in which this interaction takes place. The harvesting of prey can vary with population density, evasiveness of prey, topography, and vegetation. Additionally, prey is influenced not only by top-down processes but also bottom-up as prey species are also dependent on available food resources. It is a common misconception that systems are either solely impacted from the top down or the bottom up. These two processes are rather complementary counterflows that are inextricably linked rather than mutually exclusive. This means that trophic cascades may originate from top-down consumptive effects but are influenced by the resulting bottom-up processes. The influences that bottom-up and top-down processes have differ. The flow of resources into an ecosystem is influenced by bottom-up processes, whereas top-down processes influence how these resources are distributed within the trophic levels (Hairston et al., 1960; Terborgh & Estes, 2010).

The largest predators often exert influence over significant cascading trophic interactions, either through tri-trophic or mesopredator cascades (Ritchie et al., 2012; Ripple et al., 2014). However, predator species frequently exhibit co-occurrence patterns, which necessitate a careful evaluation of their cumulative effects on ecosystems, especially in complex systems like tropical regions (Terborgh & Estes, 2010; Ripple et al., 2014). In the neotropics, jaguar, puma as well as ocelot exhibit co-occurrence patterns. Previous research has demonstrated that the effects of multiple predators on both prey populations and broader ecosystems can exhibit synergistic interactions. Hence, it is important to consider the potential for complementarity within the top carnivore guild as well as prey guilds of a community, which can serve to the strength of trophic cascades in select circumstances (Ripple et al., 2014). For instance, in the western Amazon, jaguars heavily rely on white-lipped peccaries, as documented by Flores-Turdera et al. (2021) and Whitworth et al. (2022). However, when the population of white-lipped peccaries crashed in the Madre de Dios region of Peru, jaguar encounter rates significantly declined. Despite this, Whitworth et al. (2022) found no evidence of a trophic cascade effect, as the post-disappearance trait composition of the community did not differ significantly from the pre-disturbance community, and there was no change in the foraging guild structure. Instead, encounter rates of pumas and collared peccaries significantly increased, which suggests density compensation due to the similar niche occupation of these species to white-lipped peccaries and jaguars. The increase in encounter rates was likely the result of the release of interspecific competition and predation (Estes et al., 2011; Ripple et al., 2014).

However, as described in the indirect effects of the jaguar's disappearance, it has become apparent that (top-down) cascading effects are possible. The current situation in the Atlantic Forest will be used as an example. The Atlantic Forest is considered a highly threatened biodiversity hotspot already having lost many large mammals in most of the remaining forests, including the jaguar (Jorge et al., 2013; Paviolo et al., 2016). Jorge et al. (2013) indicated that 88 to 96% of what remains in the Atlantic Forest is suffering from trophic cascading effects through the decline of multiple mammalian species including jaguars. The increasing fragmentation of the Atlantic Forest and loss of large mammalian species, weakens the complex interaction pathways, taking away the dampening of cascading effects. The authors specifically mention cascading effects such as changes in seed dispersal patterns and community structure, density compensation, and mesopredator release. In a separate study by Terborgh et al. (2001), an experiment was conducted on islands in Lago Guri, Venezuela, that had been isolated from the mainland due to rising water levels in 1986. The study demonstrates that trophic cascades can be unleashed in the absence of top-down regulation. It was found that in the absence of vertebrate predators, the densities of prey species were 10 to 100 times greater than the nearby

mainland which suggests that predators do limit prey population. However, as described by Terborgh and Estes (2010), it should not be forgotten that trophic cascades have the potential to trigger regime transitions, and in certain cases, alternate stable states. If a stable trophic system undergoes a significant disturbance, such as the addition or removal of an apex predator, the remaining system may experience destabilization and shift into a temporary state (Terborgh & Estes, 2010). Additionally, Terborgh et al. (2001) also cautioned that the top-down and bottom-up models oversimplify the complex interactions between vertebrate predators and prey, which operate on scales beyond the scope of direct experimentation.

4. Discussion

The disappearance of jaguars from neotropical forest ecosystems has significant implications for ecosystem dynamics. This discussion section examines the observed and potential effects resulting from the absence of jaguars, considering the intricate interrelationships among species and the complex factors at play. By addressing the potential consequences of jaguar decline, light will be shed on the broader implications of (anthropogenic-driven) jaguar extirpation and its impact on neotropical forest ecosystems as a whole. Additionally, this discussion will address the potential severity of the decline based on this review's findings, while also highlighting the challenges associated with conducting such complex studies.

The challenge of studying apex predator impacts on ecosystems

Given the ongoing decline and disappearance of various apex predator populations such as jaguars, there is an immediate and pressing need to forecast the implications of their absence as drivers of ecosystem changes. However, given the intricate nature of neotropical forest ecosystems, it has been extremely challenging to comprehensively account for all potential effects, connections, and outcomes in a single review study. Consequently, this study has had to shift the focus to presenting the most prominent and plausible effects in current literature that are most evident to consider in the context of a decline in jaguar populations. It is therefore highly likely that not all factors or consequences following a jaguar decline (mainly indirect consequences) are mentioned in detail. There are still no definite and comprehensive answers available regarding the exact consequences as studies have not been able to provide these. At present, available literature simply does not have the all-encompassing answers.

Much is known about the interactions between species in an ecosystem but much less is known about the functioning of tropical ecosystems as a whole, let alone all the interactions that occur within these systems. This has left the answers to the sub-questions somewhat superficial and interpretable rather than providing direct, complete, and satisfactory answers. However, as the decline in the jaguar population continues, there has been an increase in research being carried out to study the consequences of its disappearance for conservation planning. Meaning that it is likely that the remaining knowledge gaps will be narrowed in the near future. Additionally, it is important to note that the approach of this study reviewed the ecological factors on which jaguars exert their influence individually. In all reality, however, the complexly interlinked pathways of tropical forest ecosystems make it so that all information obtained per sub-question is also interlinked. Although the sub-questions are answered as separate factors, the influences described are not stand-alone impacts and are all affected by and connected to one another as it is one complex interlinked flow of interactions.

There is lacking evidence of jaguar-specific instances. This is likely the result of it being significantly difficult to directly study the impacts of jaguars on different ecological factors within neotropical forest ecosystems. Especially in comparative studies that involve contrasting areas with and without jaguars, where the study areas cannot be entirely identical in all other ecological aspects. Additionally, it requires experimentally manipulating apex predators to directly test the impacts (Allen et al., 2014). Such studies would require a local extirpation of the predator followed by, for example, the assessment of its prey's response down to the trophic levels. However, the extirpation of the predator ironically also leads to the loss of the capacity to restore the top-down control in its entirety, which goes against the aim of said studies which is finding answers for effective conservation planning. However, the sizes and ranges of these species are very large, often on scales of tens to thousands of square kilometers, further complicating ecosystem-wide experiments. Consequently, most studies with a focus on the role

or impacts of jaguars (or other apex predators for that matter) on ecosystems are largely observational (Terborgh & Estes, 2010; Estes et al., 2011). The challenging nature of conducting species-specific studies leads to various studies basing their answers on the effects of the impact apex predators have in general, which are then connected to the possibility of the same scenarios happening, in this case, the jaguar's decline specifically. Knowledge is lacking on species-specific effects that have been tested or experimented so no definitive answers can be given on what exactly the consequences are through all trophic levels including all direct and indirect effects. Most studies being cited in recent studies have either been done on smaller species that are not as mobile, or within more isolated systems like islands, rescue centers, or smaller reserves, allowing for small-scaled manipulation, or in the case of species-specific instances, experimentation on islands from which apex predators have been extirpated such as Barro Colorado and the islands of Lago Guri (Estes et al., 2011).

Conducting these studies is further complicated by the fact that the restoration of jaguar populations does not guarantee the restoration of their full potential in providing natural ecosystem services, particularly in anthropogenic-induced fragmented and degraded forest environments. This is especially complex in tropical forest systems. Subsequent studies on the responses of local extirpations have therefore lagged for many years (Terborgh & Estes, 2010). Additionally, it is not just jaguars that are susceptible to continued anthropogenic-induced habitat fragmentation; important prey species such as the white-lipped peccary also experience population declines (Mena et al., 2020). It must therefore be considered that anthropogenic factors leading to jaguar extirpation and decline are also significantly contributing to the alteration of the neotropical forest ecosystem functioning as a whole. This and factors such as hunting and shifting land uses, as well as natural plant succession, can all have a significant and cumulative impact and in turn also complicate studies on species-specific impacts on ecosystems (Terborgh & Estes, 2010; Ripple et al., 2014).

Another significant factor that is crucial not to overlook is that predator species frequently exhibit co-occurrence patterns, which necessitate a careful evaluation of their combined effects on ecosystems. Previous research has demonstrated that the effects of multiple predators on both prey populations and broader ecosystems can exhibit synergistic interactions (Ripple et al., 2014). This shows that (1) impacts on ecosystems are rarely driven by just the actions of one apex predator alone but are rather a result of the multiple interlinked pathways, and (2) effects may be dampened as a result of synergistic interactions within complex (food)webs. However, the impacts may be induced by top-down forces.

Due to the complexity of fully comprehending the role of apex predators in natural ecosystems, much (but not all) is based on theories and likely scenarios happening in other regions and/or with other species of (felid) apex predators on different continents, linking these back to potential effects the jaguar may also have in the ecosystem they live in. And although there may be some truth to these outcomes, and they help understand likely or possible scenarios, there is a remaining incomplete and distorted picture of the influences of apex predators across natural ecosystems worldwide (Estes et al., 2011).

Trophic cascading effects and niche takeovers

Various studies indicate the potential occurrence of trophic cascades in the absence of jaguars, providing evidence of cascading effects such as increased prey species populations, the release of mesopredators, and alterations in forest composition resulting from competition and predation release (Terborgh et al., 2001; Terborgh & Wright, 1994; Ritchie & Johnson, 2009; Roemer et al., 2009; Galetti et al., 2013; Ripple et al., 2014; Prugh & Sivy, 2020). Though these outcomes differ between protected and disturbed landscapes.

Well-protected areas seem to be less likely to experience significant cascading effects as these areas allow for a full complement of prey and carnivore guilds (Steinmetz et al., 2013; McPeek, 2014). This increases the likelihood of niche expansions, density compensation, or takeovers as has been demonstrated with pumas and collared peccaries that could expand their niche in the events of jaguar and white-lipped peccary declines and extirpations (Emmons, 1987; Moreno et al., 2006 Whitworth et al., 2022; Estes et al., 2011; Ripple et al., 2014). This may dampen crash events of ecosystems, especially in complex tropical forests with numerous interactions and pathways, which could potentially function as a safety net for species extirpations or significant cascading effects (Finke & Denno, 2004; Steinmetz et al., 2013; McPeek, 2014). This means that the impact on ecosystems following a jaguar decline or disappearance may not necessarily lead to significant crash events. The effects appear strictly dependent on numerous factors such as level of area protection, habitat connectivity, prey behavior, prey and predator abundance, synergistic interactions, etc. However, anthropogenic-disturbed and fragmented landscapes can have less stable ecosystems. In these systems, there are far fewer strong interactions and full complements of prey and predator guilds are lacking. Consequently, ecosystems become much more vulnerable leaving little room for dampening of crash events. Surrogates may be less likely to be present or may not have the capacity to prevent more significant crash events leading to extirpations or significant influence on ecosystem functioning.

The understanding of all these effects is not straightforward. Identifying precise causal relationships among large carnivores like jaguars, prey species, and plants within vast and intricate systems like tropical ecosystems, poses significant challenges. Consequently, the concept of trophic cascades involving apex predators remains controversial and continues to raise many questions. Especially given that the conducted studies indicating trophic cascades lack replication and control studies (Ford et al., 2015). There is also a strong need for the understanding of all links, connections, and dynamics within a system to completely comprehend certain consequences which is a very challenging task.

Direct and indirect effects on predators, prey, and the environment

Jaguars exert top-down influences on their prey and influence co-occurring predators through interspecific competition. Their absence may indirectly lead to mesopredator release (Roemer et al., 2009), increases in prey populations (Emmons, 1987; Wright et al., 1994; Terborgh et al., 2001), and dietary shifts in predators (Emmons, 1987; Moreno et al., 2006). This can have consequences for seed recruitment and forest composition (Terborgh, 1988; Terborgh et al., 2001; Terborgh & Wright, 1994; Beck et al., 2013; Paolucci et al., 2019; Villar et al., 2020), which are intricately linked to shifts in prey behavior (Brown et al., 1999; Terborgh et al., 2001; Letnic & Dworjanyn, 2011; Oriol-Cotterill et al., 2015), and alterations in nutrient dynamics (Schmitz et al., 2010). However, this paper has not had a specific focus on the interference of anthropogenic factors in these impacts. As has been discussed before, these are largely responsible for the jaguar declines and they also play a significant role in the alterations of ecosystem functioning, which further complicates studies viewing apex predator influences specifically. In anthropogenic-disturbed areas, for example, people often experience human-wildlife conflicts with jaguars as they are known to attack livestock. Consequently, these jaguars often get killed by cattle ranchers (Polisar et al., 2003; Tortato et al., 2017).

Although several studies mention an increase in prey populations in the absence of jaguars, the interference of anthropogenic-induced habitat fragmentation could induce significant opposite impacts on these prey species. For instance, populations of native large herbivores are low in fragmented areas, even in the absence of apex predators. This is the result of overhunting and shrinkage of the remaining forest fragments (Bogoni et al., 2022). In the Atlantic Forest, large herbivorous mammals such as the white-lipped peccaries are declining due to continued habitat

fragmentation. Although there is generally lacking information on what the consequences are for seed predation in the remaining forests, Galetti et al. (2015) showed that a decline in large seed predator herbivores like peccaries resulted in competition release for smaller seed-predating rodents. Small rodents appeared responsible for the majority of the seed predation, indicating there may be consequences for natural plant-herbivore interactions. This demonstrates the complexity of studies like these and all other influences in tropical systems that must be considered when studying apex predator impacts on ecosystem functioning.

This example highlights that the combined impact of anthropogenic factors and jaguar declines in smaller-sized areas with reduced protection can result in divergent outcomes compared to large protected natural areas free from anthropogenic-induced habitat fragmentation, hunting and alternative land-uses. As a result, the observed changes in neotropical forest ecosystems within disturbed areas may deviate from the findings reported in the cited studies of this review. The severance of the direct and indirect effects resulting in jaguar declines (mesopredator release, increases in prey populations, dietary shifts in co-occurring predators, niche expansions, changes in forest composition, shifts in prey behavior, and changes in nutrient cycling) may either vary or be significantly interfered with or altered by anthropogenic disturbance. These insights further underscore the intricate nature of conducting studies in this field.

5. Conclusion and recommendations

The purpose of this study is to examine the potential consequences of the extinction of the jaguar, the largest apex predator in lowland neotropical forest ecosystems. The study aims to compile and review the current knowledge and possible scenarios surrounding the ecological effects of jaguar disappearance. The findings are crucial for developing effective conservation measures and accurately assessing the severity of the problem. The conclusions will be given in order of the sub-questions followed by the answer to the main question and recommendations for future research.

1. In what ways does the presence and absence of a jaguar influence its prey?

Jaguars are somewhat selective hunters, choosing prey based on socio-ecological factors and local availability. They commonly consume white-lipped peccaries, collared peccaries, capybaras, giant anteaters, white-nosed coatis, and nine-banded armadillos, although preferences may vary by region and prey availability. The impact of jaguars on prey populations depends on factors like prey abundance, behavior, and reproduction rates. However, the significance of jaguars' impact on specific prey species varies. Giant anteaters, with their low population density, are more significantly affected by jaguars compared to species with higher densities like capybaras or peccaries. While many species are consumed in proportion to their abundance, jaguars seem to disproportionately impact white-lipped peccary populations. Beyond direct killing, jaguars and their prey are connected through "the ecology of fear." Prey species modify their behavior, resource intake, metabolism, reproduction, foraging patterns, and habitat use in response to perceived predation risk. Capybaras and peccaries exhibit fear-induced responses in the presence of jaguars, leading to increased herding during foraging and changes in foraging patterns and distribution. Research shows that the absence of jaguars can cause predation release and increased prey numbers, resulting in changes in herd sizes and altered foraging patterns. Prey species' responses to predator absence are influenced by their unique life histories and ecological characteristics, leading to diverse pathways of change in ecological communities.

2. How could its disappearance affect other (meso)predators in the same ecosystem?

The disappearance of jaguars from an ecosystem can have significant effects on other (meso)predators. It can lead to mesopredator release and increased activity levels, potentially contributing to a decline in prey populations. The relationship between apex predators, mesopredators, and prey is complex and context-dependent, influenced by ecosystem productivity and species interactions, which is something that must be considered. Mesopredator release is expected to be more pronounced in systems with strong links between species, while high species diversity and diet breadth can dampen its effects. The impact on specific predator species varies, with ocelots showing less avoidance of jaguars and even benefiting from their presence in large, well-protected areas. Jaguars can also alter the behavior and hunting strategies of other predators, such as pumas, and induce dietary shifts in ocelots and pumas in their absence. Overall, jaguars play a crucial role in shaping the dynamics and interactions of (meso)predators in the ecosystem.

3. Could another (apex) carnivorous predator take over the jaguar's place?

The puma is the closest predator to the jaguar in the neotropical forest ecosystems and appears to be the only predator with the potential to partially fill the jaguar's ecological role. While both species tend to show mutual avoidance and have similar activity patterns, there are differences in their diets and physical characteristics. Jaguars have robust physiques and larger heads, allowing them to hunt and kill larger and more heavily armored prey, while pumas are more opportunistic feeders and consume smaller prey. Jaguars have a competitive dominance over pumas but dietary shifts and niche expansion

are possible in the absence of jaguars. A favorable characteristic of the puma is that they have the advantage of being greater generalists and more tolerant of human-altered landscapes. However, differences in diet and physical characteristics do not allow for full compensation.

4. Which indirect ecological effects on the neotropical forests are likely?

The indirect ecological effects of jaguars and other apex predators on neotropical forests are likely to be significant. These effects include changes in forest composition and seed recruitment, alterations in prey behavior, impacts on nutrient cycling, the release of invasive and exotic species, and disease regulation. Jaguars play a crucial role in shaping forest ecosystems by influencing the distribution and behavior of their prey species, thereby indirectly affecting vegetation patterns and ecosystem structure. The absence of jaguars can thus lead to shifts in forest composition, changes in prey behavior, disruptions in nutrient cycling, the proliferation of invasive species, and increased disease transmission.

5. How likely is it that the ecological effects could induce a trophic cascade?

Trophic cascades are complex interactions in food webs that involve both top-down and bottom-up processes. While apex predators like jaguars can influence cascading trophic interactions, the co-occurrence of multiple predator species and prey guilds can affect the strength of trophic cascades. In some cases, the disappearance of apex predators like jaguars can lead to density compensation and increased encounter rates of other predator species, while in others they may lead to cascading effects such as in the Atlantic Forest, including changes in seed dispersal patterns, community structure, and the release of mesopredators. It is important to recognize that trophic cascades can trigger regime transitions and alternate stable states, and the interactions between predators and prey are more complex than simplified models suggest. The occurrence of trophic cascades and the exact causal relationships are still controversial as replication and control studies are generally lacking and require further study.

What are the possible consequences for ecosystem functioning in the lowland neotropical rainforests if the largest apex predator, the jaguar, became extinct?

The absence of jaguars in neotropical forests would disrupt predator-prey dynamics, particularly affecting white-lipped peccaries. Other predators may experience mesopredator release, altering interactions within the ecosystem. While the puma could partially fill the jaguar's role, differences in diet and physical characteristics limit its ability to fully compensate. Their absence would have indirect effects on the ecosystem, including changes in forest composition, prey behavior, nutrient cycling, invasive species population, and increased disease transmission among prey. The loss of jaguars could potentially trigger trophic cascades, but the strength and occurrence of these cascades depend on various factors and are still subject to research and debate. Overall, the absence of jaguars would have significant implications for predator-prey interactions, ecological dynamics, and ecosystem structure in neotropical forests but these effects are not straightforward and depend on factors such as habitat characteristics, species composition, interactions among different organisms, and also anthropogenic influences. Understanding the effects on neotropical forest ecosystems requires considering the intricate interrelationships among species and the complex factors at play. The complexity of all interrelationships in protected tropical forest ecosystems may dampen significant influences, meaning that a jaguar decline may not necessarily lead to significant crash events. Due to the complexity of this research topic and lacking information, a full conclusive, and detailed answer to this burning question cannot be given at this moment and requires further intensive research.

While there are still knowledge gaps and challenges in conducting species-specific studies, including anthropogenic influences, ongoing research aims to fill these gaps and improve conservation planning. It is therefore recommended to continue the monitoring of crash events and changes in the wider terrestrial vertebrate community in areas where apex predators are currently significantly declining. This is crucial to understanding how these changes influence ecosystems and their services. This should be the focus of future research as this will give a better insight into the severity of effects and how to act upon these changes for more effective conservation planning to prevent further jaguar decline. Continued research in the future shall tell whether these complicated unique systems will ever be fully comprehended for the benefits of effective conservation planning for jaguars as well as co-occurring species.

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