Title: Human adaptation strategies are key to co-benefits in human-wildlife systems

Authors: Alexander K. Killion[1*], Julianna M. Ramirez[2], Neil H. Carter[1]

Author Affiliations:

[1]School for Environment & Sustainability, University of Michigan

440 Church St, Ann Arbor, MI 48109

[2]Department of Biological Sciences, Boise State University

1910 W University Dr, Boise, ID 83725

*Corresponding Author

Email Addresses: A. Killion: killion@umich.edu; J. Ramirez: julieramirez@u.boisestate.edu; N. Carter:

nhcarter@umich.edu

Corresponding Author Contact Information:

Alexander Killion

University of Michigan

Dana Building

440 Church St.

Ann Arbor, MI 48109

killion@umich.edu; Phone: 815-601-2535

Abstract

Sustainable development goals such as global food security and biodiversity conservation can conflict because these efforts create situations where humans and wildlife share landscapes, often leading to interactions that detrimentally affect both groups. Therefore, coexistence between humans and wildlife is more likely when adaptation strategies produce and sustain co-benefits, rather than benefitting one group only. However, we lack a good understanding of how different social and ecological factors contribute to co-benefit outcomes, which limits our opportunities to address local issues and scale up successful conservation actions. Here, we performed the first global review of the human-wildlife interaction literature to assess which human adaptation strategies generated co-benefits and how stakeholder involvement and other context-specific conditions mediated those outcomes. We found that active guarding, fencing, repellents, and socio-economic mechanisms consistently led to co-benefits across species and contexts. Thus, these interventions might be the best candidates for scaling up coexistence from local to regional or national scales. Surprisingly, stakeholder involvement was less consequential than other variables, yet, overall, it played an important role in sustaining co-benefits regardless of adaptation strategy or social-ecological context. We highlight future research directions to help manage tradeoffs and achieve sustainable coexistence outcomes in shared landscapes.

Introduction

Sustainable development is exceedingly difficult when multiple priorities conflict with each other. For example, expanding or intensifying agriculture to increase crop yields can potentially increase food security worldwide (Laurance, Sayer, & Cassman, 2014). However, the associated land clearing and resource competition can also lead to habitat loss and population declines of wildlife species (Wolf & Ripple, 2017). On the other hand, interactions between humans and wildlife, like large carnivores or elephants, can sometimes lead to risks to human safety (e.g., attacks on people) and livelihoods (e.g., livestock depredation or crop raiding), thereby reducing support for wildlife conservation in those circumstances (Redpath et al., 2013). Indeed, facilitating the sustainable coexistence of humans and wildlife in shared landscapes (e.g., areas where people and wildlife frequently co-occur) is a major conservation challenge globally because interventions often promote one goal at the expense of others and consequently lead to counterproductive outcomes (Carter et al., 2017; Duffy, St John, Büscher, & Brockington, 2016). Finding solutions that generate benefits for both humans and wildlife, or co-benefits, are therefore urgently needed. This is particularly evident given that the interface between human and wildlife populations continues to expand with humans encroaching into wildlife habitats, and in some cases, wildlife populations recovering and expanding back into portions of their historic ranges that are now occupied by dense human settlements (Lamb et al., 2018; Schlossberg, Chase, & Griffin, 2018).

A key to coexistence is mutual adaptations between humans and wildlife, such that both are able to change their behavior, learn from their experiences, and pursue their own interests with respect to each other (Carter & Linnell, 2016; Lute & Carter, 2020). Unlike wildlife, human adaptation strategies are subject to influence by regulation and social norms, and thus capable of being changed through concerted action (Bautista et al., 2019). By focusing on adaptations that

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underlie deep leverage points such as the design and intent of the system, long-term coexistence may be better supported (Abson et al., 2017; Hartel et al., 2019). With increasing attention on the looming extinction crisis, research on which human adaptation strategies can, or should, be adopted has become more common and elicited strong debate in the literature (Eklund, López-Bao, Tourani, Chapron, & Frank, 2017; Miller et al., 2016; Treves, Krofel, & McManus, 2016; van Eeden, Crowther, et al., 2018; van Eeden, Eklund, et al., 2018). For example, recent work recommends suspending predator control efforts that lack empirical evidence for decreasing the likelihood of livestock depredation (Treves et al., 2016). Other research suggests that producers who switch from lethal control to non-lethal methods (e.g., livestock guarding dogs) experience less depredation and financial loss (McManus, Dickman, Gaynor, Smuts, & Macdonald, 2015). In other systems, installing electric fences have proven effective in deterring hippopotamuses (*Hippopotamus amphibious*) from rice fields (González et al., 2017). Audio and visual repellents, while initially effective, were found to only deter large carnivores from livestock for a few months (Miller et al., 2016). Although recent reports provide crucial insights in how different adaptation strategies affect human outcomes, such as damages to crops or livestock, they often overlook the direct outcomes on animals and focus on single taxa (e.g., apex predators). Thus, the effects of various adaptation strategies on both humans and wildlife, across species and contexts, are unclear.

Central to discussions on the efficacy of adaptation strategies is the role of stakeholder involvement. Recent work highlights the importance of effective stakeholder participation in conservation planning to increase trust and ensure sustainable decisions are reached (Redpath et al., 2013). Who is involved and has power in the implementation of group adaptations, such as building conservation fences, is also noteworthy because defining boundaries and access rights is a highly political process (Evans & Adams, 2016). Other work underscores the importance of conservation incentives fitting within existing cultural values (Expósito-Granados et al., 2019; Hazzah et al., 2014).

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However, the numerous and often complex relationships that stakeholders can have with wildlife generate uncertainty in their role of producing co-benefits (Pooley et al., 2017). Furthermore, we have scant information on how stakeholder involvement influences the likelihood of coexistence across contexts and species, limiting the generalizability of insights. As a result, we still lack a crucial understanding of how stakeholder involvement mediates the effect of human adaptation strategies on co-benefits.

The social and ecological contexts within which human-wildlife interactions occur have also been shown to influence conservation outcomes (Lischka et al., 2018; Pooley et al., 2017). For example, forage availability and subsistence farming practices can influence crop-raiding behavior (Branco et al., 2019). Land-use and ownership can influence the likelihood of livestock depredation and the availability of methods for mitigating damage (Woodroffe, Frank, Lindsey, Ole Ranah, & Romañach, 2007). Also, institutional structures may either inhibit or encourage cross-sectoral collaboration and therefore greatly impact conservation and sustainability outcomes, although structures vary across global regions (Hartel et al., 2019). However, it is equivocal whether social and ecological contexts consistently lead to co-benefits, or lack of, across different study systems. Without a holistic evaluation of adaptation strategies capable of promoting both human and wildlife well-being, we might be overlooking opportunities to advance coexistence and reach sustainable development targets.

Here, we performed the first global review of the human-wildlife interaction literature published from 2000 to 2018 to assess: 1) how various human adaptation strategies relate to co-benefits for both humans and wildlife; 2) how adaptations that generate co-benefits differ from those that provide a benefit for humans or wildlife only; 3) how different contextual factors, such as geographic location or taxa, mediate the influence of those adaptation strategies on outcomes; and

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4) how the involvement of stakeholders in the implementation of adaptation strategies increase the likelihood of producing co-benefits in various contexts. We conclude by identifying key characteristics of those adaptation strategies that successfully lead to co-benefits and lend themselves to up-scaling, as well as provide recommendations on future research on coexistence.

Methods

Rapid Evidence Assessment

To better attribute causal relationships, we only reviewed studies that evaluated human and wildlife outcomes following the implementation of an adaptation strategy. We conducted a rapid evidence assessment (Dicks et al., 2017) of peer-reviewed literature on Web of Science and Google Scholar databases and collected articles published from 2000 to 2018 that: 1) evaluated the effectiveness of an adaptation to reduce a negative human-wildlife interaction; and 2) captured both human and wildlife outcomes (Notes S1). We defined benefits to wildlife as outcomes that did not reduce individual animal fitness; to humans as a reduction in the level of impact imposed by wildlife; and co-benefits as when both occurred simultaneously. Keywords included "humans", "wildlife", "conflict", "interact", "coexist" (among others, Notes S2). Article abstracts were read by a single author and the full paper was read if it met the inclusion criteria or was unclear. We extracted information related to the type of interaction, how an adaptation was implemented, and descriptive information about the study design and outcomes (Table S1). Ultimately, only variables which were available across all studies were included. We also relied on snowball sampling, where we included studies that were cited by selected papers in our primary search. Two coders independently classified the final articles and coding discrepancies were negotiated until a classification agreement was reached (Notes S3). Four independent reviewers were given the same classification rules and

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coded a random 10% sample of all articles, and primary coder reliability was measured using Krippendorff's Alpha (Krippendorff, 2012). We conducted a rapid evidence assessment of the literature in lieu of a meta-analysis because studies were inconsistent in their application of treatments, analyses, or measures of effectiveness, thus making it difficult to quantitatively compare effect sizes across studies. Each included study was ultimately attributed with a set of social and ecological variables where we focused on three classified outcomes: wildlife-only benefits; human-only benefits; or co-benefits. We analyzed these data by evaluating outcome likelihoods given the presence or absence of a single variable, as well as quantifying the relative effects of different variables on outcomes using random forest models and classification trees.

Outcome Likelihoods

First, we calculated the proportion of studies with each benefit outcome relative to the presence or absence of all other variables. Based on these proportions, we calculated Fisher's exact test to determine whether an adaptation strategy was significantly more likely than another to lead to a specific outcome (i.e., co-benefit). In addition to the Fisher's exact test, we calculated odds ratios to compare the odds of co-benefit outcomes when stakeholders were involved in the implementation of the adaptation versus when they were not.

Random Forest Models

We generated random forest models to compare the relative importance of variables in explaining three different outcomes: co-benefits (i.e., both humans and wildlife benefit); human-only benefits; and wildlife-only benefits. The random forest classifier relies on an ensemble of single

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classification trees and are well suited for high dimensional data and multiclass problems (Breiman, 2001; Gutiérrez, Hilborn, & Defeo, 2011). Multicollinearity of explanatory variables can influence variable importance (Nicodemus, Malley, Strobl, & Ziegler, 2010) and if two variables were found to be collinear (Cramer's V > 0.65) the variable with the fewest classes was removed (Table S2). Since the binary outcome variables were imbalanced (i.e., more benefits than losses or conversely), we balanced all model datasets to a ratio of 1:1 using the random over-sampling technique (Lunardon, Menardi, & Torelli, 2014). We then analyzed the dataset (i.e., the original or over-sampled) with the greatest model accuracy and area under the ROC curve (Fig. S1). Models were built using the "randomForest" package in R software (Liaw & Wiener, 2002; R Core Team, 2019). We grew 500 trees by examining how many trees it took to stabilize the classification rate for all models and then doubled the highest value since computational time was not a restraining factor (Fig. S2). To determine how many variables would be randomly sampled as candidates at each split, we generated five 10-fold cross validations and chose the value associated with the highest average accuracy (Kuhn, 2008). We also tested the sensitivity of tree depth (i.e., node size). Because this presented no large changes in accuracy, we chose the default value of one (Gutiérrez et al., 2011). Variable importance was measured by the percentage of mean decrease in random forest model accuracy when that variable was removed (Breiman, 2001). That is, the greater the decrease in accuracy, the greater importance that variable plays in classifying outcomes.

Classification Trees

Since random forests do not generate a final, single tree which is useful to interpret variable relationships, single classification trees were built to identify and visualize the hierarchy of categorical factors most associated with certain binary human-wildlife outcomes. Trees were built in

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R using the "rpart" package (Therneau, Atkinson, & Ripley, 2015). For each outcome model, the tree was grown to balance tree complexity with prediction accuracy (Gutiérrez et al., 2011). To ensure the final tree was not atypical and that we did not overfit the model, we performed 50 10-fold cross validations, and chose the smallest tree within 1-standard error of the lowest error rate (Breiman, 2001; De'ath & Fabricus, 2000)

Results

Adaptation Strategies

Based on outcome frequencies, 93% of cases using active guarding strategies led to co-benefits and were the most common adaptation (31%; Fig.1, Table S3). Approximately three-quarters of cases using fencing (22% of total adaptations) and 69% of cases using repellents (21% of total adaptations; Fig. 1) led to co-benefits. When a combination of multiple adaptations from the same class was used (e.g., night guarding and livestock guarding dogs) a mutually beneficial outcome occurred in 71% of the cases compared to 61% with a single technique. Based on Fisher's exact test, active guarding strategies were significantly more likely than repellents to support co-benefits given all species ($p < 0.01$), especially for large animals ($p < 0.01$).

Results from random forest models indicated the adaptation strategy was the most influential variable associated with co-benefit outcomes (Fig. 2). In the human-only model, adaptation strategy was also the most important variable, however contextual factors played a larger role in determining human-only outcomes compared to other models (Fig 2). Classification trees indicated co-benefits to be associated with active guarding (e.g., livestock guarding dogs, watchtowers, attentive herding, etc.), fencing, repellents, and socio-economic mechanisms (e.g.,

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compensation or awareness); whereas, aversive conditioning, lethal removal, translocation, and physical manipulation were associated with losses for either humans or wildlife (Fig. 3). The wildlife-only classification tree included aversive conditioning, and the human-only tree also included the physical manipulation of wildlife. Only the variable indicating the type of adaptation implemented was needed in the single classification trees, because the addition of other explanatory variables did not significantly improve model accuracy (Fig. 3).

Contextual Factors

Co-benefit percentages were highest in Africa (74%) where active guarding practices were the most commonly used adaptation (43%) and when implemented, resulted in co-benefits 91% of the time (Fig. 1). In contrast, co-benefits were the least frequent in Asia (45%) and North America (49%). In Asia, translocation was the most common adaptation strategy (32%) however it was never linked to co-benefits, while guarding strategies (14%) did every time (Fig. 1). In North America, repellents were the most common strategy (30%) and were linked to co-benefits 64% of the time, whereas fencing (15%) was less common but more consistently led to co-benefits (83%). When accounting for all variables, geographic location was among one of the strongest predictors of benefit outcomes, yet was commonly a quarter less important than the adaptation type (Fig. 2).

Among wildlife conflict activities, domestic animal predation (45%) and crop raiding (41%) were the most common, followed by food scavenging (5%), human harm (4%), property damage (4%), and disease transmission (1%). Co-benefits were achieved in 65% of animal predation studies and in 69% of crop raiding studies. The random forest models indicated that wildlife activity was a relatively strong predictor of benefit outcomes compared to the other variables, but was still commonly a quarter less important than the adaptation type (Fig. 2).

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Omnivores were the least likely group to experience co-benefits (39% of omnivore studies) or wildlife-only benefits (57%) whereas primates were most associated with co-benefit outcomes (85%) followed by carnivores (65%) and herbivores (62%; Fig. S3). In animal predation studies, 52% experienced retaliatory killing, of which 57% resulted in co-benefits following implementation of adaptation strategies. Barring stakeholder involvement, retaliatory killing, wildlife size and type were some of the least important variables for predicting co-benefits (Fig. 2).

Stakeholder involvement

Stakeholder involvement was the least important variable in the random forest models of co-benefits, when accounting for the other factors (Fig. 2). However, the odds of stakeholder involvement leading to co-benefits were 4 times greater (95% CI: 2-7) than without stakeholder involvement. Stakeholder involvement was the least important variable in the random forest models of co-benefits, when accounting for the other factors (Fig. 2). In contrast, co-benefits were more likely in Asia and North America when stakeholders were involved ($p < 0.01$; $p < 0.01$; Fig. 4). Co-benefits were also more likely to occur when stakeholders were involved when adapting to large and mega-sized wildlife ($p < 0.01$; $p = 0.04$). However, stakeholder involvement did not significantly alter the likelihood of co-benefits when grouped by type of wildlife or when sample sizes were small (e.g., South America; Fig. 4).

Discussion

Synthesizing insights of what social and ecological factors contribute to outcomes that benefit both humans and wildlife is important to enable biodiversity conservation and improve human livelihoods in shared landscapes. We found that the most influential factor in predicting co-

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benefits was the type of adaptation used. The relative importance of adaptation type for co-benefit outcomes was nearly four times greater than any other variable (Fig 2). It is encouraging that adaptation type is so strongly related to co-benefits, as it suggests that management and conservation actions (i.e. deep leverage points) have a high potential to promote coexistence outcomes. Overall, co-benefits were more likely to be produced when stakeholders were involved in the implementation of the adaptation strategy compared to when they were not. However, when compared to other factors the effect of stakeholder involvement was relatively small and the association with co-benefits was limited to specific circumstances. Below, we use our review of the literature to reveal key characteristics of adaptation strategies, contextual factors, and stakeholder involvement that contributed to co-benefit outcomes across diverse shared landscapes, and provide guidance for future work and policy supporting human-wildlife coexistence.

Adaptation Strategies

With the wide range of ways people can adapt to wildlife, and the consequences of those decisions on human-wildlife outcomes, generalizable insights on what strategies generate co-benefits is needed. We found that active guarding strategies (e.g., livestock guarding dogs, watchtowers, attentive herding, etc.) were the most common adaptation strategy and had the highest percentage of co-benefit outcomes. Although these strategies require someone to be present during vulnerable times, they were generally more effective and were so across diverse contexts including various wildlife groups, conflict activities, and geographic locations. This suggests a single adaptation can be applicable for multiple species and that more active behavior such as guarding crops from watchtowers or using livestock guarding dogs may be the most effective at generating co-benefits. However, in many communities children are responsible for guarding duties,

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which can take priority over their education. Training dogs or other guard animals (e.g., llamas; Meadows & Knowlton, 2000) have upfront training costs and maintenance, just as repellents or fences do, yet are less prone to habituation by wildlife, can deter many types of animals (Gehring, VerCauteren, Provost, & Cellar, 2010), and could relieve guarding expectations of children. Studies seldom included adaptation costs (Notes S3), which influences where certain adaptations can be implemented. For example, active guarding strategies may be a less viable option in regions with high labor costs whereas electric fencing may not be feasible in low-income areas. The length of effectiveness of active guarding strategies has also shown to vary (Khorozyan & Waltert, 2019) and owners need to be attentive of domestic guarding animals and their potential to influence other wildlife (Lescureux & Linnell, 2014). These active guarding practices were common hundreds of years ago when wildlife, specifically predators, were more abundant (Rigg et al., 2011). With the extirpation of species once competing with humans for resources, these active guarding activities have become less common, leading to aggravated conflict with predators as they recolonize or their populations grow (Gehring et al., 2010). A shift to relearning these practices may alleviate human losses and be beneficial to wildlife.

Some strategies led to co-benefits, but were less likely to lead to human-only benefits. For example, although the use of fencing and repellents were associated with co-benefits, they were significantly less likely to produce benefits for humans alone. These adaptations may have been overlooked as effective means if only human outcomes were considered. However, when accounting for the likelihood that those adaptations can also benefit wildlife, they rank as a more effective alternative. A caveat, however, is that an animal's aversive response to repellents (e.g., light or noise) can attenuate over time. Others have also noted a tradeoff often exists for the effectiveness of deterrent-based methods and the amount of time they remain effective (Miller et al., 2016), and recommend they primarily be used in times of high risk or while long-term strategies are being

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prepared (Khorozyan & Waltert, 2019). Repellents also require more sensors and devices to effectively protect a larger perimeter. Likewise, fencing costs increase with field area and might become financially infeasible in larger holdings. When materials and cost are prohibiting, fencing is primarily used to protect higher value crops, which often require more labor to grow, and thus are grown in fewer quantities and in smaller fields. However, some repellent techniques (e.g., chili powder or bees) provide additional income opportunities by selling leftover chilies or honey (King, Lala, Nzumu, Mwambingu, & Douglas-Hamilton, 2017). Fencing had limited impacts on the fitness of nearby wildlife in the studies we analyzed, but has the potential to cause negative impacts on populations or other species, for example, by fragmenting habitats and hindering migrations (Jakes, Jones, Paige, Seidler, & Huijser, 2018; Løvschal et al., 2017; Said et al., 2016). These effects were seldom accounted for in studies. Watchtowers above unfenced fields are one alternative that appear effective when spotting and manually deterring large or mega-sized wildlife such as elephants (Thapa, 2010), yet require several towers in larger fields.

Our findings suggest that lethal removal, translocation, physical manipulation, and aversive conditioning are not likely to produce co-benefits and corroborates similar doubts in effectiveness from previous studies (Boast, Good, & Klein, 2016; Miller et al., 2016; Treves et al., 2016). Translocating an animal, for example, can disrupt intra-specific interactions (e.g., territoriality; Stahl, Vandel, Herrenschmidt, & Migot, 2001) and relocated animals are likely to return to their original location (Weilenmann, Gusset, Mills, Gabanapelo, & Schiess-meier, 2010) or produce losses wherever they were moved. In other words, translocating an animal also translocates the problem (Fernando, Leimgruber, Prasad, & Pastorini, 2012). Translocation is also financially impractical for animals that occur in high densities. Although these strategies did not typically lead to co-benefits, their use is sometimes desirable or required in some cases. For example, translocation or lethal removal might be the best available method to immediately remove a large predator that is

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frequently attacking livestock or people. Furthermore, it is important to note that we defined animal

fitness at the individual level and thus all lethal removals and physical manipulations were, by

definition, classified as wildlife losses. Outcomes from these specific adaptation strategies might

have differed had we defined animal fitness as the average across the animal population. However,

we were unable to do this as the included studies rarely measured population-level effects on

wildlife.

Stakeholder Involvement

We found that involving stakeholders in the design or implementation of the adaptation was

significantly more likely to produce co-benefits. Adaptations that included stakeholders occurred

primarily in African countries and corroborates the findings of others who found stakeholder

involvement to occur more frequently in developing areas (Baynham-Herd, Redpath, Bunnefeld,

Molony, & Keane, 2018). However, the role of stakeholder engagement in specific contexts was less

clear. Despite being a common occurrence in Africa, stakeholder involvement was significantly more

likely to produce co-benefits in only Asia and North America and for large or mega-sized wildlife (Fig.

4). The non-significant addition of stakeholders or large confidence intervals within certain

contextual factors limits our understanding of what exactly about stakeholder involvement drives

co-benefit outcomes.

A common result was not that stakeholders were any better at implementing the strategy

but rather it was necessary for them to support the adaptation strategy being tested if it were to be

sustained (Hill & Wallace, 2012). Producers would stop using certain methods during the study

because they did not see the benefit, or conversely, became falsely optimistic about effectiveness

and did not remain vigilant, resulting in greater losses (Gunaryadi & Hedges, 2017). Another benefit

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of including stakeholders during the design of the adaptation strategy is the opportunity to find locally sourced alternative materials (Osborn & Parker, 2003). Building fences, bomas, or noise makers out of familiar materials may make users more likely to adopt those strategies and can reduce maintenance costs (Osborn & Parker, 2003). Others have noted conservation failures solely due to not taking a community-based approach nor resolving disagreements within communities about what drives negative outcomes (Pooley et al., 2017). Conflict displacement can also occur when not everyone in the community adapts (Carter, Baeza, & Magliocca, 2020). For example, fladry can shift depredation by wolves (*Canis lupus*) onto pastures that are not protected (Musiani et al., 2003). Similarly, depredation has been displaced to places that did not have accessibility to technologies like nighttime lights (Lesilau et al., 2018). These characteristics suggest a transdisciplinary approach is well suited for human-wildlife coexistence research (Lozano et al., 2019). Transdisciplinary research and participatory scenario planning, provide stakeholders a platform to include their perspectives, work across institutions to co-create a shared vision for the future, and supply a framework to evaluate outcomes and adapt to changes (Lang et al., 2012; Oteros-Rozas et al., 2015). In general, stakeholder involvement plays an important role in co-benefits but the studies included in our analysis were inconsistent in their specificity of involvement, making it difficult to capture nuances. This underscores the need for greater attention and better accounting of stakeholder involvement in future studies.

Contextual Factors

The production of co-benefits varied greatly depending on the contextual factors surrounding a given human-wildlife interaction. Nearly three-quarters of the studies conducted in Africa led to co-benefit outcomes. Notably, the use of active guarding strategies was quite common

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in the region (Fig. 1). In contrast, the relative paucity of co-benefits in North American studies was primarily due to the use of strategies that favored outcomes for humans only or those that were not associated with benefits for wildlife. Specifically, black bears (*Ursus americanus*) in North America were common targets of strategies that rarely generated co-benefits, perhaps because they are a highly adaptive species and learned that repellents or aversive conditioning were not life threatening. In South America, risks from wildlife to livestock and human poaching of wildlife are ongoing challenges to conservation (Ohrens, Treves, & Bonacic, 2016). However, we lacked studies from that region that met our inclusion criteria and therefore are unable to make inferences about outcomes of adaptation strategies that are consistent with our larger analysis.

Retaliatory killing is considered a major threat to species worldwide. Although we documented whether retaliatory killing occurred in the study, this variable was challenging to identify as a cause or consequence of human-wildlife interactions. Regardless, the presence of retaliatory killing had low variable importance in our random forest model, suggesting that it was not influential in delivering co-benefits, nor human-only benefits. This indicates the need to work with stakeholders to understand the multitudinous drivers of conflict (Pooley et al., 2017).

Moving Forward

There are elements of how we share landscapes with wildlife that should be considered in future work including land-tenure and planning, as well as human values and perceptions. A combination of an expanding human footprint and a growing interest in protecting areas to recover animal populations is creating more opportunities for human-wildlife interactions. In many circumstances, it is difficult to reverse land-use decisions to reduce losses and residents are left to deter wildlife forever, or adopt new livelihood strategies (O'Connell-Rodwell, Rodwell, Rice, & Hart,

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2000). Insights from sustainability and transdisciplinary sciences can help in these circumstances. For example, incorporating how likely land managers are to adopt alternative strategies can better uncover opportunities to increase spatiotemporal multifunctionality, support dynamic conservation, and coexist in shared landscapes (Killion et al., 2018). Differences in how interactions are conceptually framed can also influence the type of adaptation used and subsequent outcomes. Human psychology, broader social norms, or policies in the community or region can all influence adaptation options, the ease of implementation, and likelihood of adoption (Bennett et al., 2017; van Eeden, Crowther, et al., 2018). For example, it was found that conservation professionals favored enforcement and awareness adaptations when conflict was occurring in more highly developed countries (Baynham-Herd, Redpath, Bunnefeld, & Keane, 2019). Thus, lessons learned from sustainability science and transdisciplinary research are well suited to support human-wildlife coexistence research, practice, and policy. Greater effort is needed to capture a wider range of social and ecological factors in human-wildlife interaction studies (Ceauşu, Graves, Killion, Svenning, & Carter, 2019). Our analysis is evidence to this fact, in that the majority of studies focused on the response of wildlife to human actions, rather than factors that led to a change in human behavior (4%) and lacked rich anthropological information which limited a deeper analysis of the human variables. Labor and material costs of adaptations were rarely considered (16%) and emphasizes the need for better reporting on cost-effectiveness of preventative measures over time (Iacona et al., 2018; Kissui, Kiffner, König, & Montgomery, 2019).

Landscape-scale habitat quality and availability can affect human-wildlife interactions (Kioko, Okello, & Muruthi, 2006), and seldom did studies account for conspecifics or prey/forage abundance and availability, which could have a large impact on the frequency of livestock depredation or crop raiding. An adaptation strategy aimed to decrease depredation in an area with low prey abundance may result in lower benefits than in an area with greater prey abundance (Woodroffe et al., 2007).

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Conversely, this may not be the case if depredation in a system is opportunistically driven (Herfindal et al., 2005). Similar to other analyses, there was a bias in our analysis for studies involving large carnivores which elicit certain types of adaptation strategies as well as geographic location (Lozano et al., 2019). Future studies that adopt a standard data collection protocol (Treves et al., 2016; van Eeden, Eklund, et al., 2018), include population-level effects, and capture greater variety in geographic, socio-cultural, and types of human-wildlife interactions will help alleviate those biases in future analyses.

This work has direct implications on wildlife conservation policy. First, this research provides much-needed evidence of efficacy for different adaptation strategies, while also identifying gaps. These data can be integrated directly into adaptive governance mechanisms that require evidence-based solutions to dynamically improve sustainability outcomes (Armitage et al., 2009). Second, by identifying practices that simultaneously protect wildlife while minimizing negative interactions on shared landscapes, our results point to win-win options sought after in national- or regional-level policy frameworks and international agreements, such as the US Endangered Species Act, European Habitats Directive, and the Convention on Biological Diversity. Third, focusing on co-benefits better accounts for trade-offs in different strategies, helping design more successful and longer-lasting benefit-transfer mechanisms. Many studies consider effective implementation of benefit-transfer mechanisms, such as performance payment schemes (Zabel & Holm-Müller, 2008), as key to promoting coexistence in areas that disproportionately incur costs from wildlife (O'Bryan et al., 2018). Lastly, by synthesizing social and ecological factors and focusing on co-benefits, our study provides a useful template for a broader research agenda that informs the eventual development of national-level coexistence policy based on cross-sectoral collaboration, adaptive governance, and a more comprehensive set of performance indicators. Such an effort could be modeled on the legislation of the Collaborative Forest Landscape Restoration Program aimed to accelerate and

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financially support monitoring and collaboration across communities, organizations, and agencies (Butler & Schultz, 2019).

Conclusion

Finding ways to create co-benefits on shared landscapes has the potential to advance sustainable development goals. We found that adaptations based on improving active guarding strategies were most likely to result in co-benefits. Adaptations based on improving responsible animal or crop production behavior are low-cost, easy to adopt, and have potential to provide the foundation for humans and wildlife to sustainably share landscapes around the world. These findings represent positive elements (or bright spots) of existing practices which support a good Anthropocene, as well as areas needing additional research (Bennett et al., 2016). Since this was a global analysis, our inferences are not intended to be used for making specific site recommendations, as each system can have a unique host of complex conditions. Instead, this work addressed the need to capture trends in efficacy that can be scaled to, and tested on, many different landscapes with similar characteristics. Transdisciplinary planning efforts coupled with stakeholder-driven adaptations to anticipate and respond to change holds promise in promoting human-wildlife coexistence.

Acknowledgments and Data

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Author Contributions

A.K., J.R., and N.C. developed the study design and performed the review. A.K. conducted all analyses. A.K., J.R., and N.C. drafted the manuscript.

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Figure 1. Count of studies in each region and type of adaptation strategies used. Bars above the line indicate studies that produced co-benefits, bars below the line indicate those that did not.
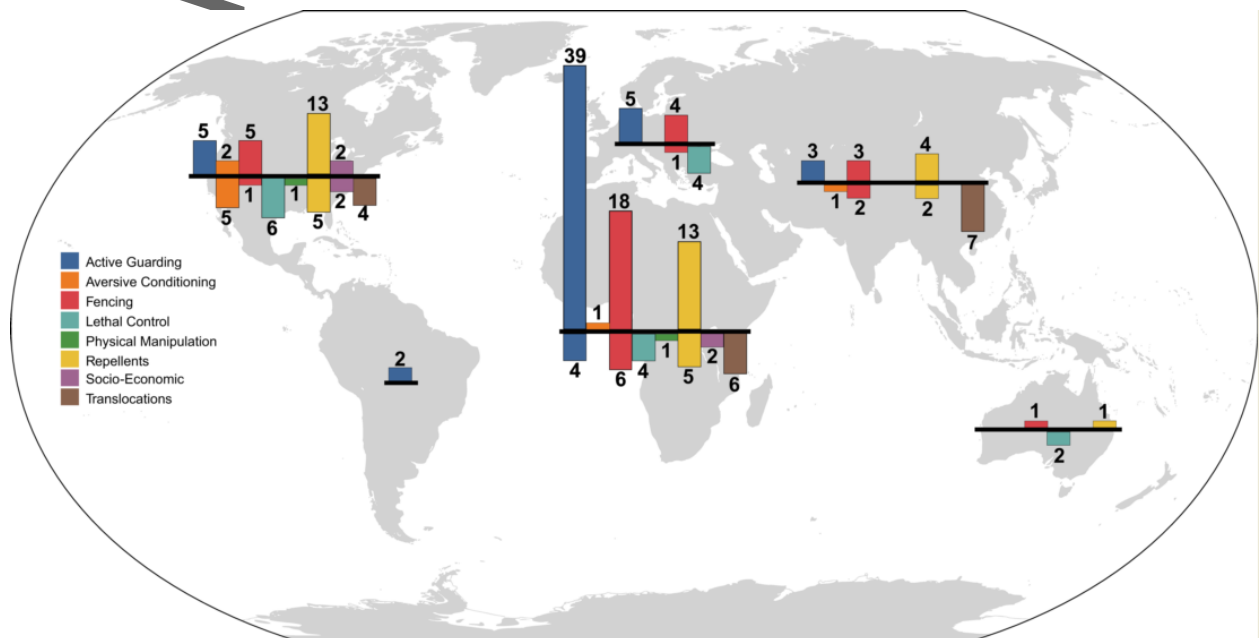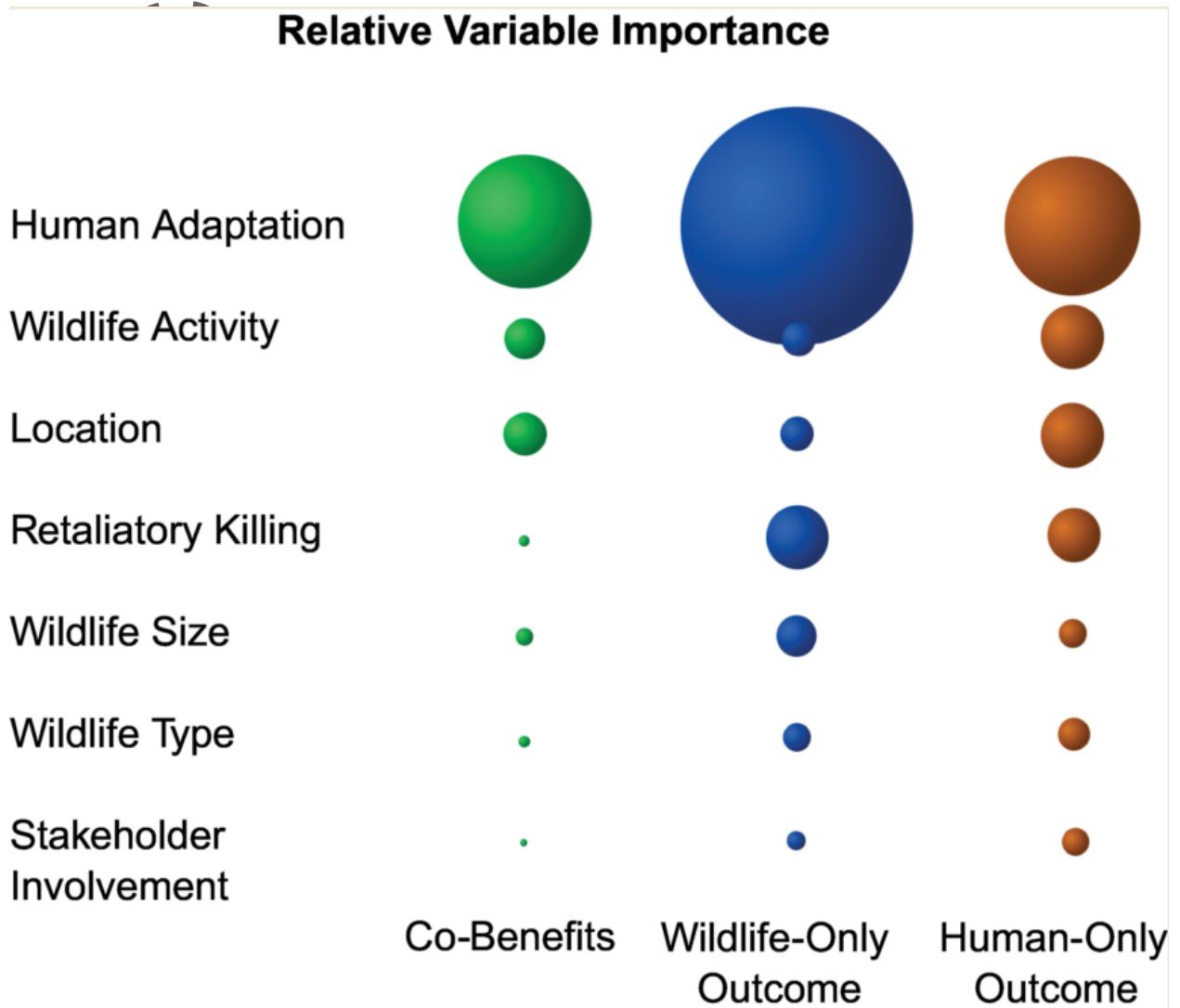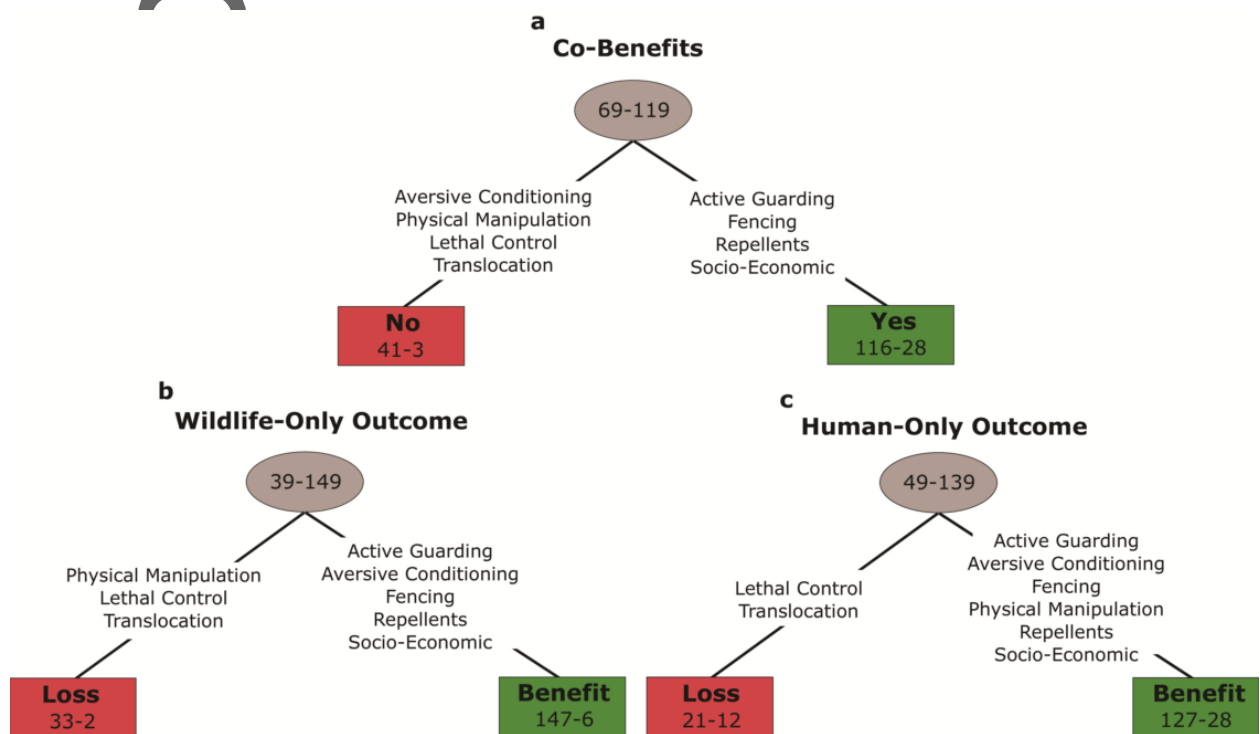
Figure 2. Relative variable importance values to explain each binary outcome, determined by random forest models. The area of the bubbles is proportional to the mean decrease in model accuracy. For example, the size of the bubble for human adaptation in the co-benefits model indicates that it is over four times more important than wildlife activity when predicting co-benefit outcomes (i.e., co-benefits or not). Wildlife- or human-only outcomes were either benefits or losses.
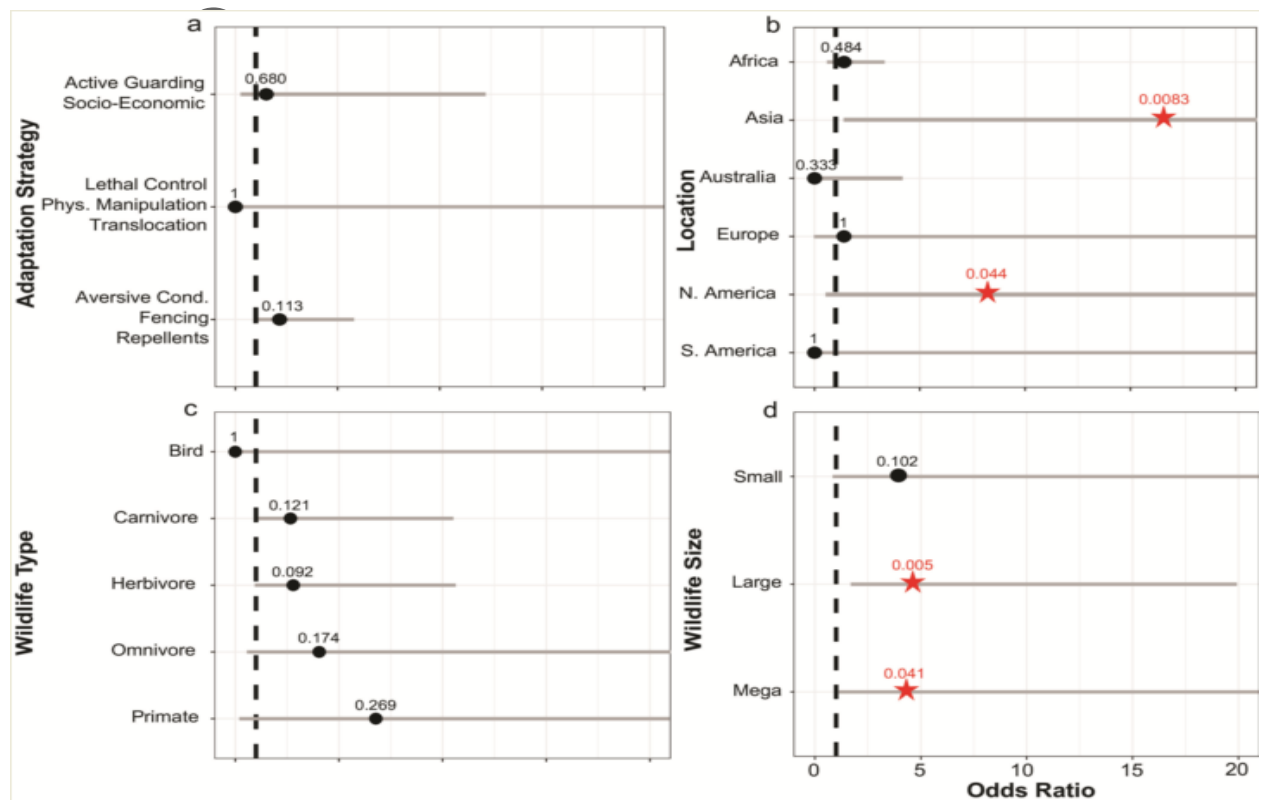

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Figure 3. Pruned single classification trees for models of (a) co-benefits, (b) wildlife-only outcomes, and (c) human-only outcomes. The only variable selected for in all models was the type of adaptation strategy used. Values in boxes indicate number of studies in each node. First number is the count of studies with that node outcome.

Figure 4. Odds of co-benefit outcomes when stakeholders are involved in the adaptation process compared to when they are not. In panel (a), adaptations were grouped based on similarities in approaches to increase sample size. Fisher's exact tests were used to produce p-values (value provided above odds ratio dot, red star when significant; $p < 0.05$) and 95% confidence intervals (gray lines). The black dashed line indicates odds ratio of one.