REVIEW

Conservation Biology

Joining forces toward proactive elephant and rhinoceros conservation

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Article impact statement: Habitat assessments should be inclusive, collaborative, and equally value ecological and anthropogenic factors to be proactive.

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Abstract

Proactive approaches that anticipate the long-term effects of current and future conservation threats could increase the effectiveness and efficiency of biodiversity conservation. However, such approaches can be obstructed by a lack of knowledge of habitat requirements for wildlife. To aggregate and assess the suitability of current information available on habitat requirements needed for proactive conservation, we conducted a systematic review of the literature on elephant and rhinoceros habitat requirements and synthesized data by combining a vote counting assessment with bibliometric and term maps. We contextualized these numeric and terminological results with a narrative review. We mapped current methods, results, terminology, and collaborations of 693 studies. Quantitative evidence for factors that influence the suitability of an area for elephants and rhinoceros was biased toward African savanna elephants and ecological variables. Less than one third of holistic approaches considered equal amounts of ecological and anthropogenic variables in their assessments. There was a general lack of quantitative evidence for direct proxies of anthropogenic variables that were expected to play an important role based on qualitative evidence and policy documents. However, there was evidence for a segregation in conceptual frameworks among countries and species and between science versus policy literature. There was also evidence of unused potential for collaborations among southern hemisphere researchers. Our results indicated that the success of proactive conservation interventions can be increased if ecological and anthropogenic dimensions are integrated into holistic habitat assessments and holistic carrying capacities and quantitative evidence for anthropogenic variables is improved. To avoid wasting limited resources, it is necessary to form inclusive collaborations within and across networks of researchers studying different species across regional and continental borders and in the science-policy realm.

KEYWORDS

Ceratotherium simum, Dicerorhinus sumatrensis, Diceros bicornis, Elephas maximus, evidence-based conservation, habitat assessment, Loxodonta, Rhinoceros

Colaboración de Fuerzas hacia la Conservación Proactiva de Elefantes y Rinocerontes Resumen: Los enfoques proactivos que anticipan los efectos a largo plazo de las amenazas a la conservación actuales y futuras podrían incrementar la efectividad y la eficiencia de la conservación de la biodiversidad. Sin embargo, dichos enfoques pueden ser frenados por una falta de conocimiento de los requerimientos de hábitat para la vida silvestre. Para sumar y evaluar la idoneidad de la información disponible sobre los requerimientos del hábitat necesitados para la conservación proactiva realizamos una revisión sistemática de la literatura sobre los requerimientos de hábitat de los elefantes y rinocerontes y sintetizamos los datos combinándolos en una evaluación de conteo de votos con mapas bibliométricos y de términos. Contextualizamos estos resultados numéricos y terminológicos con una

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revisión narrativa. Mapeamos los métodos, resultados, terminologías y colaboraciones actuales de 693 estudios. La evidencia cuantitativa de los factores que influyen sobre la idoneidad de un área para los elefantes y los rinocerontes estuvo sesgada hacia los elefantes de la sabana africana y las variables ecológicas. Menos de un tercio de las estrategias holísticas consideró cantidades iguales de variables ecológicas y antropogénicas en sus evaluaciones. Hubo una carencia generalizada de evidencias cuantitativas para los indicadores directos de las variables antropogénicas que se esperaba tendrían un papel importante con base en la evidencia cualitativa y los documentos de las políticas. Sin embargo, hubo evidencias de una segregación en el marco conceptual entre los países y las especies y entre la ciencia versus la literatura política. También hubo evidencias de un potencial sin explotar para las colaboraciones entre los investigadores del hemisferio sur. Nuestros resultados indicaron que el éxito de las intervenciones de conservación proactiva puede incrementarse si las dimensiones ecológicas y antropogénicas se integran a las evaluaciones holísticas del hábitat y si se mejoran las capacidades de carga holísticas y las evidencias cuantitativas de las variables antropogénicas. Para evitar gastar los recursos limitados, es necesario formar colaboraciones inclusivas dentro y a lo largo de las redes de investigadores que están estudiando a diferentes especies en las fronteras regionales y continentales y dentro del ámbito de la ciencia política.

PALABRAS CLAVE

conservación basada en evidencias, valoración del hábitat, Ceratotherium simum, Dicerorhinus sumatrensis, Diceros bicornis, Elephas maximus, Loxodonta, Rhinoceros

INTRODUCTION

Effective nature conservation requires evidence-based management decisions (Pullin et al., 2004) and appropriate prioritization of problems for which limited resources are allocated (Game et al., 2013). Although immediate threats to the survival of species require the crisis-solving abilities of reactive conservation science (Kareiva & Marvier, 2012), proactive conservation could further increase conservation effectiveness by providing greater flexibility toward future scenarios (Freudenberger et al., 2013) and reducing costs (Drechsler et al., 2011). Proactive conservation aims to recognize potential threats to vulnerable species and use this to avert negative impacts and buffer against future pressures by applying strategic foresight (Cook, Inayatullah, et al., 2014). Research contributing to proactive conservation aims to be timely (Sutherland et al., 2011), includes a dynamic definition and perspective on nature and human drivers (Pressey et al., 2007; Svenning, 2018), focuses on processes rather than patterns (Thuiller et al., 2008), and has a forward-looking perspective that considers multiple potential futures (Cook, Wintle, et al., 2014). The underlying objective of proactive conservation can be to protect areas that are under low threat, but are irreplaceable (Brooks et al., 2006), to prevent the degradation of not nearly extinct species (Seddon et al., 2014), or to restore degraded habitats or extirpated species or functional types (Svenning et al., 2016). Proactive conservation goes beyond the protection of species from extinction and aims to achieve viable and ecologically functional populations (e.g., the International Union for Conservation of Nature [IUCN] Green List [Akçakaya et al., 2018; Grace et al., 2019]). One type of proactive approach is trophic rewilding, which aims to restore top-down trophic interactions and self-regulation of ecosystems by introducing or reintroducing species (Svenning et al., 2016).

However, to achieve proactive conservation it is necessary to identify areas for potential range extension (Zarzo-Arias et al., 2019). To predict—or conserve—the future of a species, one thus needs to understand what makes an area suitable for a species (Thuiller et al., 2008). Therefore, a clear understanding of the habitat requirements of these species is needed.

The persistence of a species depends not only on ecological habitat suitability, but also on societal support for the species and for conservation generally (Carpenter et al., 2000). This is in particular the case for proactive interventions that have a long-term perspective, such as reintroductions, translocations, and land-use planning for human–wildlife coexistence (Svenning & Faurby, 2017; König et al., 2020). Understanding and including these human dimensions in habitat and species management can improve conservation outcomes (Behr et al., 2017). However, conservation efforts to protect rhinoceros and elephants are increasingly accompanied by the use of force and a fortress mentality, potentially alienating those communities whose support could be vital to conservation success (Duffy et al., 2014; Büscher, 2015; Witter & Satterfield, 2018).

Ecological carrying capacity is still the main focus in conservation interventions, in particular with regard to introductions or reintroductions (Oginah et al., 2020). Several anthropogenic counterparts have been proposed (Decker & Purdy, 1988; Carpenter et al., 2000; Zinn et al., 2000; Kleiven et al., 2004), yet a spatially explicit analysis of human acceptance is rarely combined with ecological habitat assessments (Behr et al., 2017). This can impair the ability to conserve nature proactively because social–political objections can prevent the reintroduction of certain species from being considered in some landscapes despite ecological suitability (Behr et al., 2017). Although the importance of anthropogenic factors is often acknowledged in reintroduction policy and management plans, their importance relative to ecological factors is not explicitly stated and appears overshadowed by environmental considerations (Dublin & Niskanen, 2003; Emslie et al., 2009). Yet, to increase effective prioritization in conservation, it is important to be explicit and transparent about value judgements in order to allow for critique and adjustments (Game et al., 2013). Therefore, we aimed to further a conceptual framework and a habitat assessment approach that explicitly takes anthropogenic factors into account. We used elephants and rhinoceros as focal species because holistic habitat suitability assessments that explicitly include anthropogenic factors are especially important for species that are strongly affected by humans, such as rhinoceros and elephants, due to aspects such as resource competition and poaching (Ferreira et al., 2017; Chase et al., 2016).

Our definition of holistic carrying capacity includes both ecological carrying capacity and anthropogenic carrying capacity. The term carrying capacity can be associated with assumptions on static animal numbers and a productionist view (Ferreira et al., 2015). However, we do not consider that carrying capacity describes the maximum environmental load needed to trigger population control (Hui, 2006). Instead, we describe carrying capacity as "the capability of land to maintain and produce animals" (Hobbs & Hanley, 1990). We consider a holistic carrying capacity an indicator of the potential species densities in an area based on ecological and anthropogenic variables. This indicator can inform introductions or reintroductions by exposing which ecological and anthropogenic factors, and in which areas, conservation efforts should focus on to improve species density potentials. Animal density can play an important role in proactive conservation because it is related to several measures of habitat suitability and population viability, such as home ranges, resource selection (Horne et al., 2008), population dynamics (Wato et al., 2016), and functional effects of a species on ecosystems (Rooney & Waller, 2003). Both ecological and anthropogenic factors can drive occurrence and abundance of a species. Although ecological factors play an important role in determining elephant occurrence on a continent scale, elephant density can be more strongly determined by anthropogenic factors (de Boer et al., 2013). Similarly, anthropogenic factors, such as poaching, are dominant drivers of the widespread rhinoceros extirpation (Emslie et al., 2016).

To contribute to proactive and evidence-based conservation, we conducted a systematic review of habitat requirements and carrying capacity for all extant elephant and rhinoceros species (Pullin & Knight, 2001; Sutherland et al., 2004). We used a research weaving approach in which we combined a vote-counting assessment with bibliometric and term maps to visualize the relationships between published terms contextualized with a narrative literature review (Nakagawa et al., 2018). This assessment could reveal insights on the interactions between ecological and social science on this topic, or lack thereof, and reveal opportunities for improvement (Lawton, 2007). As terminology and methods used may differ strongly by species, region, and field, we provide bibliometric and context maps in an attempt to expose underlying reasons for such differences (van Eck & Waltman, 2010). We thus aimed to uncover the research networks through which these results came about.

In particular, we examined geographical divides in collaboration networks (Wishart & Davies, 1998; Wilson et al., 2016).

We assessed the different habitat suitability proxies and research methods used to determine elephant and rhinoceros habitat requirements; determined which anthropogenic and ecological factors influenced rhinoceros and elephant habitat suitability; determined whether there were differences among conceptual frameworks for research on habitat suitability between different study species and regions; and determined whether collaborative research networks of elephant and rhinoceros experts explained conceptual patterns observed in analyses of habitat requirements.

DATA COLLECTION

We conducted a preliminary search that aimed to determine the terminology used in studies providing information on elephant and rhinoceros habitat requirements and combined these terms with all extant elephant and rhinoceros species in our systematic search (details of literature search in Appendix S1). In our method, we followed the guidelines from Pullin and Stewart (2006). We excluded papers published in irrelevant fields or without relevant knowledge (Appendix S1), leaving 504 peerreviewed papers in our final database, out of which we could extract 693 pieces of evidence (hereafter studies). We extracted the following data from each paper: study species; proxies used for habitat suitability; methods used; type of evidence provided (see "DATA CLASSIFICATION" below); types of statistical analyses; factors included in tests and whether their effect on the habitat suitability proxy was positive, negative, or insignificant; scale of study site (district, park, region, country, multiple countries, continent, world); year of publication; topic of publication; and journal and affiliation of first authors.

Some documents presented results for several species, several habitat suitability proxies, or different categories or evidence strength. We considered a paper to include several distinct studies if there were separate dependent variable tests included. Specifically, we separated information on species, habitat suitability proxies, and evidence quality (see "DATA CLAS-SIFICATION" below). For example, a paper could include separate information on African savanna elephants (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) and studied home range and plant use or included statistical evidence and descriptive results. Because we could not treat these together, and each of these options had separate independent and dependent variables, we entered these as separate studies. Additionally, we searched for gray literature by using a snowball technique; we included 32 gray literature sources in our database.

To allow for meaningful comparisons among studies and generalizations across studies, we grouped the methods mentioned in the studies (Appendix S2). We also grouped habitat suitability proxies that were strongly linked in order to reduce the overall number of proxies and increase the amount of information per category (Appendix S2). Finally, we categorized the explanatory variables analyzed that influenced these habitat suitability proxies into groups (Appendix S2).

TABLE 1 Factors that influence habitat suitability according to narrative literature review of peer-reviewed and gray literature (Appendix S5) and 504 peer-reviewed articles that include information on habitat suitability for all elephant and rhinoceros species

Category	Habitat factor		
Ecological explanatory variables	Type, browse quantity, tree or forest cover, dense undergrowth, secondary forest, browse quality, habitat heterogeneity, grass, normalized difference vegetation index (NDVI), fire, soil quality, terrain or rockiness, water availability or distance to water, rainfall, temperature, intraspecific competition or density dependence, interspecific competition, area size or density, disease		
Anthropogenic explanatory variables	Roads; human population density; settlements; human presence; livestock; poaching; country; habitat fragmentation; crop consumption, property damage, or conflict; fences; intrinsic, cultural, or religious value; management budget or number of staff; community involvement; financial or perceived benefit; financial cost; stakeholder involvement; education; age; gender; awareness of human–elephant conflict (HEC) issues and mitigation methods; size of farm; awareness of conservation issues; income or gross domestic product (GDP); antidevelopment sentiment; membership environmental society; interest in using or visiting nature; occupation or livelihood strategy; management failure; attitude; ethnicity; human footprint; armed conflict or civil unrest; corruption, rule of law, stability, or state fragility; global ivory price		

DATA CLASSIFICATION

We classified each of the studies in our database based on whether it tested the effect of environmental or anthropogenic habitat explanatory factors on habitat suitability proxies. When a study tested both environmental and anthropogenic factors, we classified the study as holistic. The categories ecological, anthropogenic, and holistic are mutually exclusive. Within these groups, we further classified each paper into one of three types of study design: study design provided quantitative (statistical) evidence concerning habitat factors and focused on our study species (T1), provided quantitative evidence, but not specific to our study species (T2), or provided descriptive information (T3). This assessment was purely in relation to our specific meta-analysis purpose and was not used as an indicator of the quality of research or the usefulness of the research in general. We considered T3 papers to be as important in assessing and understanding habitat suitability as T1 and T2 documents. We scored each of the 693 studies on the information they provided about the influence of each of these factors (Table 1) on the habitat suitability proxy (positive, negative, and insignificant). We did not include more detailed information on the types of models and analyses used in providing the evidence (Appendix S2).

BIBLIOMETRIC AND CONTEXT MAPS

We used the bibliometric mapping software VOSviewer to construct our bibliometric and context maps (van Eck & Waltman, 2010). This software produces visualizations of similarities between authors or terms by presenting these objects in such a way that the distance between any pair of objects reflects their similarity as accurately as possible (Appendix S1). For the construction of content maps, we included terms that had more than or equal to five occurrences and belonged to the category of the 60% of terms with the highest relevance, excluding generic terms. We visualized collaborative networks of the main experts in the fields based on the country of origin of their first affiliations instead of personal names.

HABITAT SUITABILITY PROXIES AND RESEARCH METHODS

Without taking species into account, it was possible to group habitat suitability proxies analyzed in the 693 studies into 17 types (Figure 1a), of which two were strongly linked to anthropogenic factors, namely, attitude and human-wildlife conflict, the terms most commonly used in the studies included to describe complex issues related to human-wildlife coexistence. A broad variety of factors were studied as habitat suitability proxies, most of which described the use of habitat by the animals (n =127), their density (n = 80), or plant use (n = 78), followed by human-wildlife conflict (n = 68) and population dynamics (n= 61) (Figure 1a). Only 27 studies actually contained the term habitat suitability as their research subject. The least studied topics were vegetation quantity (n = 2) and intra- and interspecific competition, both had five studies. A positive effect on habitat suitability does not indicate a positive effect on the species survival and thriving for all proxies.

By far most studies analyzed targeted African savannah elephants (45.3%, n = 314) (Figure 1b), whereas <2% of the studies contained information on habitat suitability proxies for both Sumatran (*Dicerorhinus sumatrensis*) (n = 12) and Javan rhinoceros (*Rhinoceros sondaicus*) (n = 8). Similarly, for both greater one-horned rhinoceros (*Rhinoceros unicornis*) (n = 37) and white rhinoceros (*Ceratotherium simum*) (n = 36) only around 5% of the studies contained information on habitat suitability. Asian elephants (*Elephas maximus*) were the second most studies species (17.0%, n = 118), followed by black rhinoceros (12.7%, n = 86) and African forest elephants (*Loxodonta cyclotis*) (11.8%, n = 82).

Most studies used direct observations to determine which factors influenced the habitat suitability proxies (Figure 2). When it came to the use of informants, elephant research dominated. By far most of the collar studies (e.g., GPS [global positioning system] or VHF [very high frequency] collars) and studies that used spatial data, such as RS (remote sensing) or GIS (geographic information system) data, also involved African savannah elephants. The more elusive species in denser vegetation, such as African forest elephants, Asian elephants, Sumatran rhinoceros, Javan rhinoceros, and Greater **FIGURE 1** Counts of each habitat suitability proxy per elephant and rhinoceros species (*n* = 693) (HWC, human–wildlife conflicts). Detailed definitions of terms are in Appendix \$2





one-horned rhinoceros, were more frequently studied through spoor analyses. Finally, black rhinoceros research dominated ecological habitat assessment studies.

ANTHROPOGENIC AND ECOLOGICAL FACTORS INFLUENCING HABITAT SUITABILITY

Study classification

Most of the information we gathered was descriptive and therefore classified as T3. The T1 studies most often tested the role of ecological factors on habitat suitability proxies or were holistic (Figure 3). Studies only focusing on anthropogenic factors were more often descriptive without statistical evidence present to verify the suggested importance of factors. Overall, only 18% (n = 126) of the studies across species included only social–anthropogenic factors, whereas 43.4% (n = 301) focused only on ecological variables. Although there were many holistic studies (H) (n = 267), only 29.9% of these included an equal balance of quantitative evidence for anthropogenic and ecological variables. Although we know that the influence of human factors on habitat suitability is complex (De Boer et al., 2013), in these holistic studies, the choice of anthropogenic spatial layers was often simplified to a proxy for the presence of humans (e.g., roads n = 59, settlements n = 52, agriculture n = 33, population density n = 27). However, some studies included a more dynamic and complex perception of the role of humans (e.g., Chen et al., 2016). Examples of studies with balanced numbers

of ecological and anthropogenic factors tended to emphasize identifying corridors and migration routes for conservation purposes (Galanti et al., 2006; Pittiglio et al., 2012), to analyze poaching patterns (Maingi et al., 2012; Zafra-calvo et al., 2018), or to analyze understanding of the influence of both ecological and anthropogenic factors on species distribution and occupancy (De Boer et al., 2013). Most studies were conducted at district, park, or country levels (n = 616). Nine papers analyzed habitat suitability proxies on a worldwide scale, 24 papers on a continent scale, and 44 included multiple countries. Of the studies on district, park, or country levels, 57.6% included double or more the amount of ecological relative to anthropogenic factors. On continental and multiple-country scales, there was a stronger focus on anthropogenic factors; 54.1% and 50% of all studies, respectively, included double or more the amount of anthropogenic factors compared with balanced and ecologically focused studies. On a global scale, this was vice versa; 66.7% of the studies were ecologically focused.

Habitat requirements

Across studies on all elephant and rhinoceros species, we found more empirical evidence for ecological factors than for anthropogenic factors (Figure 4). Empirical evidence for the influence of anthropogenic factors on habitat suitability was especially lacking for white, black, Sumatran, and Javan rhinoceros (Appendix S3). This is in contrast with the emphasis on anthropogenic factors affecting these species' habitat suitability, as suggested by the (qualitative) heat maps and narrative review



FIGURE 2 Distribution of research methods used to gather rhinoceros and elephant habitat requirement data (n = 693) for each rhinoceros and elephant species. Gridlines are marked in groups of eight studies. Information on method categories is in Appendix S2

(Appendix S3). This could be a reflection of rhinoceroses' confinement to protected areas, relative to elephants that in general share more land and resources with humans. Nevertheless, all rhinoceros species were subject to poaching risks, despite the limited information and quantification of this threat in the scientific literature, especially for Asian rhinoceros (Haryono et al., 2016). For most of the anthropogenic factors (e.g., agriculture, settlements, roads, protected areas, and habitat fragmentation) (Figure 4a), there was a lack of consistent effect among the three effect categories (positive, negative, or not significant). This is related to the large variety of habitat suitability proxies and their interpretation and could indicate that the influence of these factors is context dependent. There also appeared to be a lack of quantitative evidence for these factors, reflecting a similar pattern as witnessed in Figure 3. Table 2 lists factors for which we did find quantitative evidence and factors with either a few quantitative studies, suggesting a potential effect, or with qualitative evidence, indicating a role of the factor in determining habitat suitability (Appendix S3). For ecological factors, there were several that consistently had significant effects across studies, and amounts of evidence were similar among quantitative, qualitative, and potential evidence (Table 2; Appendix S3).

Attitude as a proxy for habitat suitability and an influencing factor

The role of the attitude of people coexisting with elephants and rhinoceros in habitat assessments studies was twofold. Some studies measured the influence of people's attitudes on habitat suitability, whereas other studies considered attitude a habitat suitability proxy in its own right. The studies that we grouped as using attitude as their dependent variable studied the factors that influenced the attitude of people coexisting with the species, their perception of the species or conservation in general, their willingness to pay for the conservation of the species, or their perceived benefits from living with it. Researchers who included attitude in their independent variables referred to the attitude of people coexisting with the species or their acceptance, fear, or (cultural) tolerance toward it (Appendices

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FIGURE 3 (a) Frequency of studies on elephants and rhinoceros species by study category (E, studies that describe ecological factors; S, studies that describe social–anthropogenic factors; H, studies that include both ecological and social–anthropogenic factors [i.e., holistic]) per species (n = 693 studies) (1, studies focused on the species included in this study and provided statistical evidence; 2, studies that provide statistical evidence, yet were not specialized on our study species; 3, studies that provide descriptive information on the study species habitat suitability) and (b) frequency of each study category by study focus

TABLE 2	Ecological and anthropogenic factors that based on the vote-counting assessments have a positive (+) or negative (-) effect on habitat suitability for
elephant and r	hinoceros species

Factor	Quantitative evidence ^a	Qualitative or potential evidence ^b
Anthropogenic	Benefits from conservation (+)	Assign intrinsic value to species (+)
	Pastoralism (–)	Attitude of coexisting people (+)
	Human activities (–)	Awareness of conservation status (+)
		Involvement in conservation efforts (+)
		Law enforcement (+)
		Protected status/area (+)
		Railways ()
		Deforestation (-)
		Fences (-)
		Human–wildlife conflicts (–)
		Poaching (-)
		Habitat fragmentation (–)
		Political instability (–)
Ecological	Water (+)	Forest (+)
	Rainfall (+)	Wetlands (+)
	Grass quantity (+)	Grass quality (+)
	Browse quantity (+)	Shrubs (+)
	Browse quality (+)	Soil quality (+)
	Slope (-)	Reintroductions (+)
	Elevation/topography (-)	Male:female ratio (–)
		Interspecific competition (–)
		Intraspecific competition (–)
		Invasive vegetation (–)

^aResults based on factors with strong support from the quantitative data set (article types T1 and T2 [see Methods]) (Figure 4).

^bPotential results from the quantitative data set supplemented with results from the qualitative data set (table 3 in Appendices S3).

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Habitat suitability proxies

FIGURE 4 (a) Anthropogenic and (b) ecological factors and their average influence on different measures of habitat suitability according to 439 statistical tests from the 693 studies on elephant and rhinoceros habitat requirements (positive, evidence showed significant positive influence of factors on habitat suitability proxies; not significant, results not significant; negative, significant negative results; squares, combinations of factors and habitat suitability proxies; shading, the darker the color, the greater the proportion of studies that reported the specific results the square represents [i.e., saturation indicates the amount of evidence available for the importance of each explanatory variable for each of the habitat suitability proxies]). Studies included either focused on elephant or rhinoceros species specifically and provided statistical evidence or provided statistical evidence, yet were not specialized on our study species. Results that show within-study inconsistency are omitted; see Appendices S2, S3, and S5

S2 and S3). This dual application of attitude indicates both the importance and the complexity of the role that people's attitudes play in elephant and rhinoceros habitat suitability. The attitude of people toward rhinoceros and rhinoceros poaching in particular is expected to determine the ability of the species to persist in an area (Emslie et al., 2009; Haryono et al., 2016; Rookmaaker et al., 2016). The lack of direct, long-term social and economic benefits to those coexisting with these species and the framing of rhinoceros as "luxuries that exist only for the enjoyment of wealthy foreigners (or White citizens)" can compromise conservation efforts (Emslie & Brooks, 1999, p. 69). At the same time, people's attitudes toward elephants are shaped by local context and coexistence experiences with elephants (Kaltenborn et al., 2006). Elephants affecting crops and property, injuring people, or even the perceived impact of elephants can lead to reduced support for their existence (Gillingham & Lee, 2003; Maingi et al., 2012). Support for the conservation of elephants and rhinoceros can increase with increased legal economic benefits, provision of alternative livelihoods (Witter & Satterfield, 2018) (e.g., by promoting ecotourism [Yamagiwa, 2003]), and ensuring that benefits are equitably and widely distributed (Groom & Harris, 2008) (Appendix S5). Ecotourism initiatives could provide alternative livelihoods (Ogutu, 2002), yet a comanagement approach seems to be in order in which tourism is focused around the experience of local connections with their natural surroundings (Parr et al., 2008; Morais et al., 2018; McMurdo Hamilton et al., 2020). Local support for conservation initiatives can be further encouraged by effective support of and investment in those rural communities living in close proximity to elephants (Yamagiwa, 2003), especially when it comes to mitigation measures (O'Connell-Rodwell et al., 2000; MacKenzie, 2012). Community involvement in decisionmaking (Witter & Satterfield, 2018) and combatting poaching (Maingi et al., 2012) can also promote positive attitudes toward the species. The distribution of conservation knowledge could also reduce poaching (Yamagiwa, 2003); however, cultural context and relevancy should be considered key. It becomes clear from our literature analyses that the (potential) importance of these factors, often described in policy documents (Appendix S5), is not clearly reflected in research efforts and quantitative results.

DIFFERENCES AMONG CONCEPTUAL FRAMEWORKS OF RESEARCH ON HABITAT SUITABILITY

Visualization of the terms occurring in the literature on elephant and rhinoceros habitat suitability indicated strong clustering around four main themes (Figure 5 and Appendix S4). Cluster A in Figure 5 is dominated by population dynamics and population management terms relating to conservation interventions such as translocations and has a strong link to publications on black rhinoceros habitat suitability. This is also the cluster that has the strongest link to the term *carrying capacity* (Figure 5b). Especially African rhinoceros habitat suitability assessments are primarily based on population size estimates and growth rates Conservation Biology

and the evaluation of ecological carrying capacity (Emslie et al., 2009) (Appendix S5).

Cluster B is mainly dominated by terms describing vegetation characteristics and seasonal changes in these (Figure 5). This cluster has a strong link to both white rhinoceros and African savannah elephant. Both species include large proportions of grass in their diet and are seasonally dependent on grass (Codron et al., 2006; Verdaasdonk, 2018). This could explain the strong links between these species names and terms related to seasonal change to habitat and food provision (i.e., because grass quantity and quality often varies strongly and seasonally in savannah ecosystems) (Vogel et al., 2020; sections 5.1-5.3 in Appendix S5). This second cluster on vegetation and seasonal changes is strongly linked and partly overlaps cluster C (Figure 5), which is focused around movement characteristics. Again, this cluster was particularly dominated by savannah elephants. Most collar data originated from studies on African savannah elephants (Figure 3), likely explaining their strong link.

Finally, cluster D (Figure 5) had a stronger focus on humanelephant coexistence and conflicts, which coincided with the occurrence of terms originating from the anthropogenic habitat factors and social science research methods (e.g., surveys and interviews) (Figure 3). Cluster D is strongly linked to Asian elephants, which could be explained by the high occurrence of human-elephant coexistence problems across the Asian continent. Anthropogenic factors are reported to have a strong influence on elephant habitat suitability across the Asian continent in terms of elephant effect on resources humans value and human effect on elephant habitat and safety (e.g., Studsrød & Wegge, 2009; Wilson et al., 2013; Gunaryadi et al., 2017) (section 5.5 in Appendix S5). However, it is counterintuitive that the link between cluster D and other elephant and rhinoceros species is not stronger because in each of the studied species, habitat suitability was suggested to be strongly influenced by humans (Appendix S5). When we overlaid the average date of the use of terms and removed the terms themselves and standardized the size of the nodes, clusters A-D also corresponded to different average publication dates (Figure 5c). There was a noticeable shift from traditional ecological research on population dynamics and vegetation characteristics (cluster A and B) to novel research methods making use of GPS collars and spatial analyses (cluster C) and social and holistic science research providing knowledge on human-elephant coexistence and conflicts (cluster D).

RESEARCH COLLABORATION NETWORKS

The collaboration networks based on country of first author's affiliation indicated strong collaboration links from the United States and Europe to a range of countries in the Africa and Asia, as well as between the United States and Europe (Figure 6a). However, the U.S. nodes did not have a strong connecting role in the network. Instead, central roles connecting clusters within the network were occupied by European institutions. Importantly, formal collaborations were lacking between Africa



FIGURE 5 Linkages of terms used in the literature on elephant and rhinoceros habitat requirements based on titles and abstracts of the articles in the database (n = 504): (a) terms clustered (A–D) based on strength of co-occurrence of terms within clusters, (b) term *carrying capacity* featured, and (c) average time of occurrence in the literature

and Asia and between countries within these continents (Figure 6a). Especially within Asia, there were national clusters of neighboring countries studying the same species that shared only one or two author links across borders.

This lack of collaboration among researchers in the southern hemisphere was even clearer when we compared the countries where research institutions are based with those where research is conducted (Figure 6b). Malaysia, Indonesia, South Africa, India, and Ghana conducted most of the research in these countries themselves. Sri Lanka, Tanzania, Botswana, and Zimbabwe all contributed to research in their own countries and other countries. There appeared to be several strong ties between pairs of countries from the Global North and Global South, respectively, for example, Nepal–Norway, Namibia–Germany, and Botswana–England. South Africa was the only country that has elephants and rhinoceros and conducted research in other countries with these species. The United States, the United Kingdom, and the Netherlands all had a widespread presence of research projects across countries with elephants and rhinoceros, although there was a strong focus on countries and regions on the African continent.

This indicates a strong dependence on a Global North-to-South knowledge transfer and a lack of South–South knowledge transfer. The lack of South–South collaborations corresponds with other trends, such as the weak South–South knowledge exchange between countries on climate change knowledge (Pasgaard et al., 2015). The patterns we found may relate to similar socioeconomic and political factors as those related to the distribution of climate change knowledge, such as GDP (gross domestic product), school enrolment, and expenditures on education, research, and development and political stability (Pasgaard & Strange, 2013). Such factors could affect the

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FIGURE 6 (a) Collaborations (coauthors) between experts on elephant and rhinoceros habitat requirements (more than three publications on this topic) and (b) connections between countries of origin of research institutes and countries or regions where research was conducted (n = 504). Countries with the same shades are part of the same collaboration cluster

knowledge cocreation that could come from improved collaboration (e.g., increased value of knowledge due to a more diverse knowledge base), cumulative results instead of partial results, and a more critical examination of theory and paradigms across fields (Karlsson et al., 2007).

CONCLUSIONS

According to our assessment, quantitative knowledge on habitat suitability is ecologically biased for all elephant and rhinoceros species based on the type of studies, methods, habitat suitability proxies, and factors included in research publications. Our results suggest a crucial role of the acceptance of coexistence with wildlife in determining habitat suitability. Therefore, apart from (dynamic) forms of ecological carrying capacity, a holistic carrying capacity measure is needed that includes the potential density of animals possible given the societal setting, including what people are willing to coexist with. Yet, when combining anthropogenic and ecological factors in analyses, factors representing the human role in habitat suitability were often simplistic or indirect (e.g., indicating human presence only). When assessing drivers for species distribution, it is optimal to use as direct proxies as possible (Guisan et al., 2017). This requires one to identify the direct anthropogenic drivers and find suitable spatial proxies to include these (e.g., Watmough et al., 2019), for which we discovered limited evidence. Our results show there is an urgent need for more data on habitat suitability for Asian rhinoceros (Cédric et al., 2016); most of the knowledge we found was focused on African species. Besides these knowledge gaps, other factors, such as political will toward the conservation of elephants and rhinoceros, are likely to be critical in addressing the complex and holistic threats they face (Chhatre & Saberwal, 2005; Visseren-Hamakers et al., 2012). Efforts to study and address these political challenges are needed for proactive conservation and the safeguarding of these species.

Assessing the terminology diagrams showed a divergence in terminology across species. For example, black rhinoceros were associated with an ecological carrying capacity framework (Emslie et al., 2009). Although this measure of ecological carrying capacity focusing on vegetation characteristics is central in current management practices (Dublin & Niskanen, 2003; Emslie et al., 2009), other factors could have more influence on individual habitat selection, habitat preference, and plant preference by rhinoceros at low rhinoceros densities (Morgan et al., 2009).

Tapping into our demonstrated unrealized potential of across country and across continental collaborations could provide synergies to address urgent knowledge needs. The promotion of South–South collaborations requires structural changes in, for example, education, research and development, funding flows, data access and ownership, and editorial processes, in order to make networks and their outcomes available on relevant research, policy, and management levels. International organizations and institutions working on conservation could facilitate these greater South–South collaborations by making this a focus in their efforts (e.g., working groups under IUCN or Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES]). This will further advance conceptual frameworks and methods. Because we found differences in knowledge available from peer-reviewed literature and gray literature in line with previous research (Linklater, 2003), there should also be creative thinking on how to bridge the perceived boundaries between science and policy (Gieryn, 1983; Sutherland et al., 2011), and this starts by understanding each other's conceptual frameworks. Our results also showed unbalanced and underutilized collaboration networks. We acknowledge our own shortcomings and encourage others to reflect on their own research practices (Pasgaard et al., 2017; Brittain et al., 2020) and to take steps to actively bridge spatial and disciplinary collaboration gaps toward stronger proactive conservation. To realize this potential, we suggest seeking collaborations across geographic, cultural, and socioeconomic divides, engaging with local researchers, and being proactive in facilitating research capacity-building and knowledge sharing at the research location (Karlsson et al., 2007).

As we show, the potential for increased inclusivity goes beyond engaging in diverse collaborations. Inclusivity, openness, and democracy should be key objectives (Sutherland et al., 2011), and conservation professionals should communicate effectively, explain transparently, and engage over the long term with policy makers and implementers (Pressey et al., 2007). To protect elephant and rhinoceros species from extinction, proactive integrative policies that include all drivers of species and habitat loss and minimize trade-offs between species protection and sustainable development, allowing both nature and humans to thrive, are needed (Mace et al., 2018; Lindsey et al., 2020). A proactive conservation perspective is key because dynamic natural and anthropogenic processes are equally important to include in research and management plans so that conservation interventions are effective (Pressey et al., 2007). Conservationists need to consider the people coexisting with animals and to listen and integrate their opinions in each step of management plan and policy development and implementation (Cassidy & Salerno, 2020; McMurdo Hamilton et al., 2020) and gradually move toward a more active, transformative, and empowering participatory approach (Cornwall, 2008).

Ecological and human dimensions need to be linked in research (Teixeira et al., 2020), include perspectives of people coexisting with species (McMurdo Hamilton et al., 2020), and involve transdisciplinary and science-policy-management collaborations (König et al., 2020). This includes taking the complexity of human-wildlife coexistence beyond tangible costs and benefits (König et al., 2020) and acknowledging and addressing the inequality in the distribution of costs and benefits of coexisting with wildlife; these aspects need to be at the center of management and policy plans and implementation (Jordan et al., 2020). Although we summarized which factors potentially influence the acceptance of wildlife by people coexisting with them, quantitative support for the relationships between experienced benefits and conflicts of living with wildlife, social acceptance of wildlife, and subsequently people's behavior toward wildlife and conservation success is still needed. Therefore, we see a double opportunity for ecologists and social

scientists alike to acknowledge the benefits of interdisciplinary collaborations and jointly learn from each other's views and research practices to better reflect the challenges and opportunities in conservation and restoration guidelines. It is time to advance proactive conservation and restoration research, protocols, and interventions by addressing these issues together.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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