



Mapping the connectivity–conflict interface to inform conservation

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Balancing the competing, and often conflicting, needs of people and wildlife in shared landscapes is a major challenge for conservation science and policy worldwide. Connectivity is critical for wildlife persistence, but dispersing animals may come into conflict with people, leading to severe costs for humans and animals and impeding connectivity. Thus, conflict mitigation and connectivity present an apparent dilemma for conservation. We present a framework to address this dilemma and disentangle the effects of barriers to animal movement and conflict-induced mortality of dispersers on connectivity. We extend random-walk theory to map the connectivity–conflict interface, or areas where frequent animal movement may lead to conflict and conflict in turn impedes connectivity. We illustrate this framework with the endangered Asian elephant *Elephas maximus*, a species that frequently disperses out of protected areas and comes into conflict with humans. We mapped expected movement across a human-dominated landscape over the short- and long-term, accounting for conflict mortality. Natural and conflict-induced mortality together reduced expected movement and connectivity among populations. Based on model validation, our conflict predictions that explicitly captured animal movement better explained observed conflict than a model that considered distribution alone. Our work highlights the interaction between connectivity and conflict and enables identification of location-specific conflict mitigation strategies that minimize losses to people, while ensuring critical wildlife movement between habitats. By predicting where animal movement and humans collide, we provide a basis to plan for broad-scale conservation and the mutual well-being of wildlife and people in shared landscapes.

human-wildlife coexistence | landscape planning | dispersal | coadaptation | Markov chains

Coupled human–natural systems are integral to effective conservation across much of the planet (1). Protected areas—focused on decoupling nature and negative human influences—have undoubtedly benefited species worldwide (2), but faced with size limitations and increasing isolation, they may be an insufficient conservation solution (3). Shared human–wildlife spaces outside protected areas, therefore, have a vital complementary role to play in maintaining connectivity, or functional linkages between populations and habitats, so as to augment species persistence, strengthen ecosystem health and resilience, and mitigate negative impacts of climate change (4, 5). However, dispersing animals can come into direct contact with people or utilize human resources in shared spaces, leading to negative interactions or conflict to the detriment of both people and wildlife (6, 7). Facilitating human–wildlife coexistence in shared spaces is thus a concomitant conservation goal (8, 9). Reconciling these two critical requirements (i.e., managing conflict and facilitating connectivity; Fig. 1), which are seemingly at odds with each other, is one of the greatest current challenges to conservation in shared landscapes (10, 11).

Connectivity is determined by interactions between dispersing organisms and the landscape (12, 13). However, humans can transform these interactions (14). Conflict, due to its influence on animal use of shared spaces, has received recent attention as an important anthropogenic factor that can shape connectivity (11, 15). This may manifest due to risks that wildlife perceive from human presence and activities (16–18), antagonistic behavioral responses of people (e.g., chasing animals), or infrastructure (e.g., fences) for conflict mitigation (10, 19). An extreme response to conflict is the removal of “problem” animals through conflict-induced retaliatory killing, capture, or culling (6, 20). Removal imposes a demographic cost on species, as it can cause an increase in population mortality rates or change the demographic composition of a population (21), which is distinct from conflict-induced nonlethal responses that alter dispersal paths (15). This distinction between lethal and nonlethal effects of human activities has been previously considered in studying species space use (22), but has only recently been integrated into connectivity models (23). Animal movement can also exacerbate conflict (9) and determine its spatial patterns (24), such that incorporating movement ecology could vastly improve conflict

Significance

Human–wildlife coexistence is emerging as a central goal for both conservation and human well-being. Animals require movement between habitats for persistence. However, animals can come into conflict with people while dispersing. Conflict leads to loss in human lives and livelihoods, disrupts animal dispersal, impedes connectivity, and causes wildlife mortality. Thus, conflict mitigation and connectivity are seemingly at odds with one another, presenting a dilemma for conservation. We provide a framework that addresses this dilemma, which enables tailoring of conservation interventions to minimize conflict-induced losses while allowing wildlife connectivity. We illustrate this framework with the endangered Asian elephant and conflict that arises as elephants disperse out of protected areas. Our framework works toward simultaneously achieving wildlife and human well-being goals.

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predictions, and thereby its effective mitigation. Despite this potential, the problem that conflict and removal of dispersing animals presents has not been reconciled in conservation.

Here, we extend a framework for connectivity that is derived from random-walk theory to address the problem of connectivity and human–wildlife conflict. Our framework a) includes ecological underpinnings of animal movement into conflict predictions and b) assesses connectivity while considering the spatial patterns of conflict in situations when conflict imposes lethal effects on dispersing animals. Our framework maps the connectivity–conflict interface, or areas where frequent animal movement can lead to conflict, and conflict, in turn, can impede connectivity. We illustrate our framework with the example of the endangered and wide-ranging Asian elephant *Elephas maximus*, an animal for which both connectivity and conflict mitigation are urgent conservation priorities (10). By mapping the connectivity–conflict interface across a shared landscape that is home to the most abundant wild elephant population in Asia (25), we predict conflict hotspots, validate these predictions against independent reports of conflict, and identify where connectivity is lost from conflict in the region.

Results

Calibrating a Connectivity–Human Conflict Model. We extend recent developments in connectivity modeling to identify likely locations where elephants dispersing from protected areas may encounter humans, potentially leading to negative interactions and conflict. Our framework extends random-walk theory with

Markov chains that explicitly acknowledge the potential for “absorption” (26), such as mortality or removal from human–wildlife conflict. We extend the spatial absorbing Markov chain (SAMC) framework to simultaneously allow probabilistic accounting of movement behavior, mortality risk, and potential conflict for dispersers across landscapes (23).

We applied our SAMC framework to the Mysore Elephant Reserve (ER), an important conservation landscape in southwestern India that encompasses multiple protected areas and reserve forests, surrounded by a nonhabitat agricultural matrix (*SI Appendix, Fig. S1*). Connectivity among the protected areas in the ER is a recognized conservation need (25), and the region faces high levels of conflict (27, 28). We calibrated the SAMC using empirical data collected around three key elephant populations in the ER (See *Methods*); these key populations serve as points of origin of dispersal, or populations from which dispersing elephants can emigrate. In our landscape, key populations were within five protected areas (*SI Appendix, Fig. S1*). These also served as populations where elephant immigration could occur. Based on 9,100 interviews of residents of this area, we recorded 2,662 (29% of total interviews) reports of elephant use of the matrix. Of the people who reported elephant presence in their vicinity, 1,804 (68%) reported human–elephant conflict. We used this information to create maps of “landscape resistance” that reflect expectations on elephant movement (*SI Appendix, Fig. S2A*) and maps of “conditional conflict,” or conflict given that elephants use that location (*SI Appendix, Fig. S2B*). Landscape resistance is commonly used in connectivity mapping to capture the extent to which locations are impermeable to animal movement (29); here,

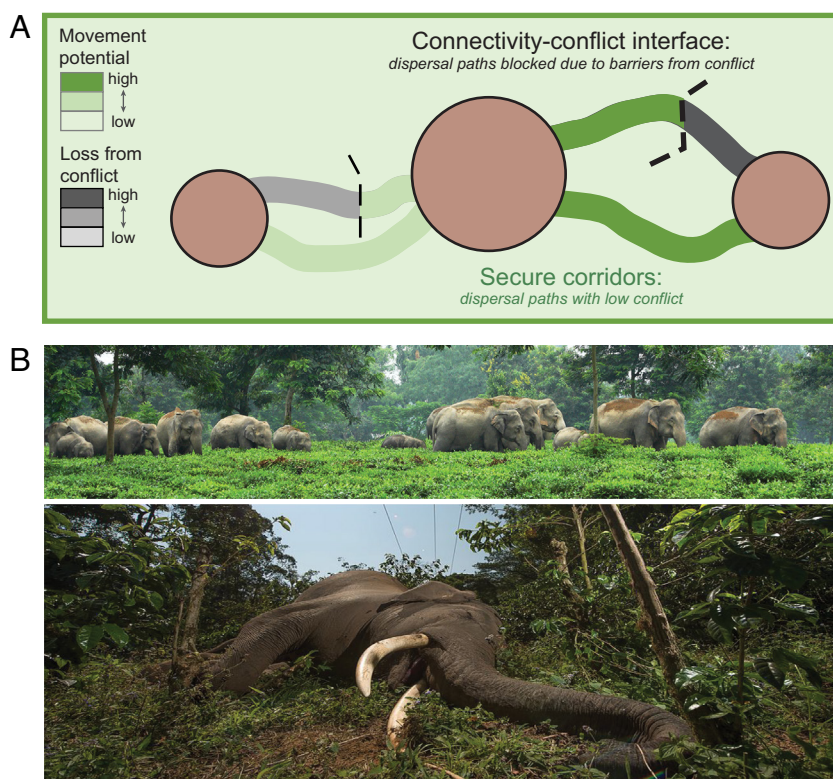


Fig. 1. (A) Human–wildlife overlap outside protected areas and the connectivity–conflict interface. The landscape includes dispersal paths between protected areas (brown nodes, with the larger node as the location from where individuals disperse) that vary in the rate of movement by animals (*Left* paths illustrate lower rates of movement than *Right* paths). Areas where movement rates along paths are high and conflict is low can be considered “secure corridors” that function as key areas for maintaining connectivity. Yet in some locations, conflict (shown as a dashed line) can arise as animals disperse across landscapes, which may block successful movement between protected areas, what we term the “connectivity–conflict interface.” Conservation strategies at the interface need to reduce conflict while maintaining connectivity. (B) Asian elephants move through human land uses and often face risks of mortality due to conflict (here, from an electrified fence). Photo credits: Bhavendu Joshi/Conservation Initiatives (*Top*); Kalyan Varma, CC BY-SA 4.0 via Wikimedia Commons (*Bottom*).

the inverse of the probability of elephant use of the landscape is used to parameterize resistance (29–31). The SAMC couples expectations from these maps to provide an integrated perspective on predicting movement and conflict across landscapes.

Based on interviews, we found that landscape resistance was determined by land use and human population density (*SI Appendix, Table S1*): elephants avoided areas with high human population density, and used croplands (finger millet, horse gram etc.), followed by agroforest plantations (such as coffee and rubber) and open plantations (coconut and areca nut; *SI Appendix, Table S2*). We found that land use and human population density also explained conditional conflict (*SI Appendix, Table S3*). Locations with coconut and areca nut plantations had higher conditional conflict compared with croplands and agroforest plantations such as coffee. Conditional conflict probability was positively associated with human population density, albeit weakly (*SI Appendix, Table S4*). Based on these findings, we mapped predicted landscape resistance and conditional conflict probability across the Mysore ER, which were positively correlated ($r = 0.73$; *SI Appendix, Fig. S2*). This relationship indicated that landscape resistance was high in areas where potential conflict was high, or, in other words, our expectation based on this model is that elephants tended to avoid moving through areas of high potential conflict. Finally, we incorporated these predictions and estimates of annual mortality rates taken from the literature (32) into the SAMC (23) to capture resistance, conflict, and natural mortality risks that may emerge while dispersing (See *Methods*).

The Connectivity–Conflict Interface. The SAMC framework can quantify a variety of metrics related to movement, demography, and connectivity across landscapes. Here we extend the SAMC to predict net visitation rates [or movement paths, analogous to “current density” in circuit theory (33)] in the Mysore ER (Fig. 2*A* and *SI Appendix, Fig. S3*). In this situation, net visitation rates quantify the expected net movement rates of dispersing individuals through a given pixel in a landscape based on specific starting and ending locations (34). Both mortality and conflict together reduced expected movement and connectivity between key populations, decreasing predicted net visitation rates (*SI Appendix, Fig. S3*). Models that did not account for mortality and conflict predicted that there would be movement across all populations in the landscape (*SI Appendix, Fig. S3A*); but connections between populations were lost when these dispersal costs were accounted for (*SI Appendix, Fig. S3 B–D*). Highest visitation rates occurred with low resistance and low conditional conflict (*SI Appendix, Fig. S4A*). The loss in visitation rates due to conflict occurred even in locations where predicted conflict was relatively low (*SI Appendix, Fig. S4B*).

We map the connectivity–conflict interface in Fig. 2*B*, distinguishing hotspots of conflict that experience high visitation rates from those with low visitation (Fig. 1). Hotspots of the connectivity–conflict interface occurred around protected areas harboring relatively large populations of elephants that were surrounded by agricultural lands (*SI Appendix, Fig. S1*).

We also predict conflict probabilities across the region over the short (1-y) and longterm using the SAMC framework which explicitly accounts for elephant movement (Fig. 3). Spatial patterns of conflict predicted by the SAMC model differed substantially from maps of conditional conflict (*SI Appendix, Fig. S2B*) and were largely concentrated around populations (Fig. 3).

Validating Conflict Predictions. Connectivity models can suffer from poor predictive capacity and a large amount of uncertainty (35). Consequently, predictions of connectivity models should be validated with relevant independent information (36). We

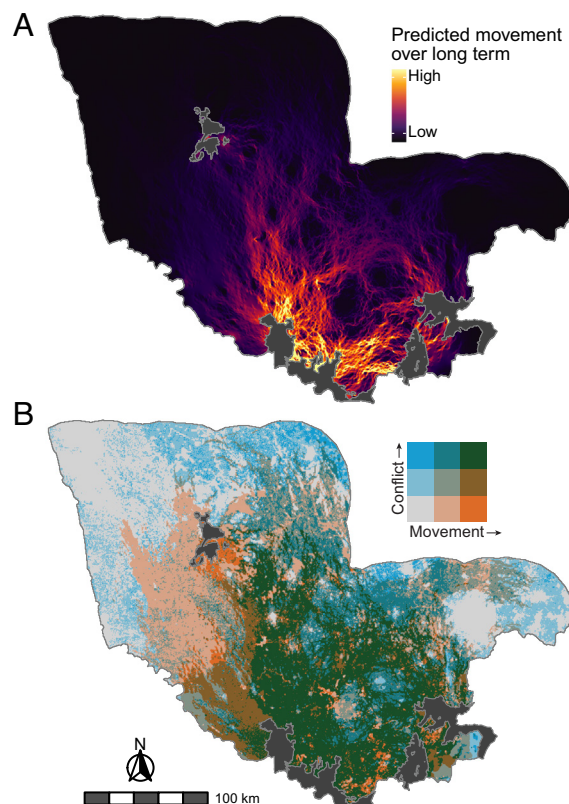


Fig. 2. (A) Predicted net visitation (movement) rate from the SAMC model incorporating both natural and conflict-induced mortality, and (B) the connectivity–conflict interface. For (B), we discretized predictions using the three quantiles for both conflict predicted from the SAMC model (measured as a probability; Fig. 3) and net visitation (measured as the expected net movement rates through pixels) to identify areas of relatively high expected conflict and movement rates.

validated both long-term predictions for expected conflict (**B**) and time-specific predictions (**B_t**) from the SAMC model with two sources of information: 1) a separate survey on human–elephant conflict of 1,102 respondents in the region ($n = 329$ records of conflict within 1 y, $n = 571$ over a 10-y period) and 2) 1,095 media reports of conflict from February 2013 to January 2016.

SAMC-derived predictions of conflict were two to three times greater in locations where conflict occurred than in locations where conflict did not occur, based on validation data from the questionnaire survey; conflict predictions were 14 times greater in the locations of elephant mortality reported in the media compared with background points (Table 1). We also compared the performance of conflict predictions from the SAMC model (Fig. 2) and that of a species distribution model (SDM) that predicts the distribution of conflict based on the joint probability of elephant use of the matrix (information used to generate resistance) and conditional conflict, in explaining variation in reported conflict. The primary difference in the SAMC and SDM models is that the SAMC incorporates the explicit movement process into conflict predictions whereas the SDM does not. Models that incorporated SAMC-predicted probability of conflict as a covariate fit the data better than the SDM based on model selection criteria (1 y: $\Delta AICc > 25.5$; 10 y: $\Delta AICc > 60.5$; *SI Appendix, Table S5*), provided more precise predictions of conflict over 1 y and 10 y, and explained 2.5 to 5 times the variation as the SDM (Fig. 4 and *SI Appendix, Table S5*).

Based on 951 records of conflict from media reports, including crop loss, property damage, human-induced elephant mortality,

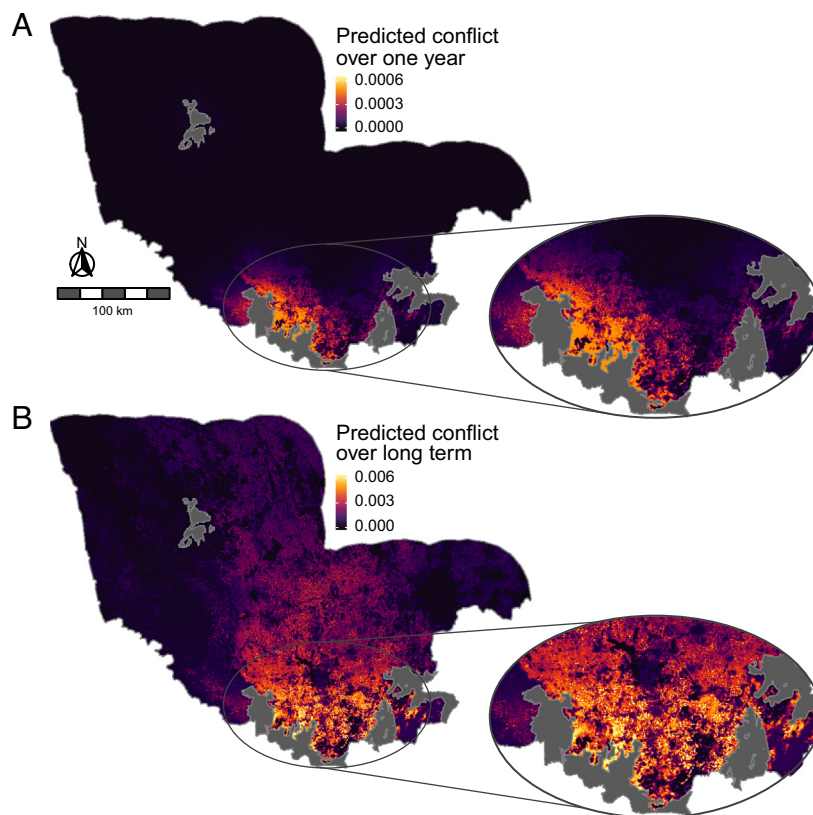


Fig. 3. Predicted conflict probability from dispersing elephants from key populations (gray polygons) over (A) 1 y and (B) the long term.

elephant-induced human mortality, and elephant captures, we compared SAMC model predictions for conflict at these points, considering them as “presence-only” data (37), and compared them with 10,000 randomly selected background points. Overall, we found moderate discrimination performance of our model based on the AUC statistic and the True-Skill Statistic (Table 1). When we segregated validation points as per the type of conflict, the model provided more accurate predictions for mortality-based

conflict than conflict when only crop damage occurred (Table 1). In general, the model was more accurate for short-term predictions than long-term predictions (Table 1).

Discussion

The Connectivity–Conflict Interface. Conflict and connectivity are clearly emerging as interconnected challenges for wildlife conservation across multiple-use landscapes. While connectivity and coexistence with people are crucial for species persistence in heterogeneous landscapes, they present a conservation paradox: connectivity enhances wildlife viability, but dispersal through human spaces can elevate conflict and mortality risk (9). Our work confronts this paradox (Fig. 1) and provides an approach to identify locations where connectivity conservation and conflict mitigation strategies need to coalesce (Fig. 3B). Our approach of formalizing and combining these ideas into a single framework demonstrates the feasibility and benefits of jointly considering conflict and connectivity, in terms of greater insights and predictive accuracy, with broad implications for science and conservation in coupled human–natural systems.

Decomposing Causes of Dispersal Failure. We extend the SAMC framework to accommodate multiple risks to wildlife—from natural mortality and conflict—when modeling species movement across landscapes. This can be relevant for multiple reasons.

First, mortality from different causes may have different intensities and ignoring these can lead to inaccurate predictions of connectivity (23, Fig. 3). For the levels of conflict-induced mortality we modeled, natural mortality had a greater impact overall in reducing connectivity across the landscape (*SI Appendix, Fig. S3*), simply because, in our case, the per-pixel probability of natural mortality was higher than that for conflict mortality.

Table 1. Validating predictions of conflict from the connectivity model, including both time-specific (1-y) and long-term predictions

Validation data	Time-specific predictions			Long-term predictions		
	AUC	TSS	Ratio	AUC	TSS	Ratio
Questionnaire around protected areas						
Observed conflict over the past year	0.68	0.25	2.41	0.64	0.20	1.91
Observed conflict over the past 10 y	0.74	0.29	3.08	0.70	0.22	2.30
Media reports						
All	0.67	0.19	5.01	0.61	0.06	1.92
Crop damage	0.65	0.15	4.45	0.61	0.07	1.82
Human and elephant injury or mortality	0.71	0.35	6.34	0.65	0.10	2.23
Elephant mortality	0.91	0.69	13.99	0.77	0.36	4.25

Shown are results assuming an annual survival rate of 0.97 (32) and a range of conflict intensities (27). We show Area under the ROC Curve (AUC), True Skill Statistic (TSS), and the ratio of average model predictions at conflict locations to average predictions at background (for media reports) or non-conflict (for questionnaire records) locations.

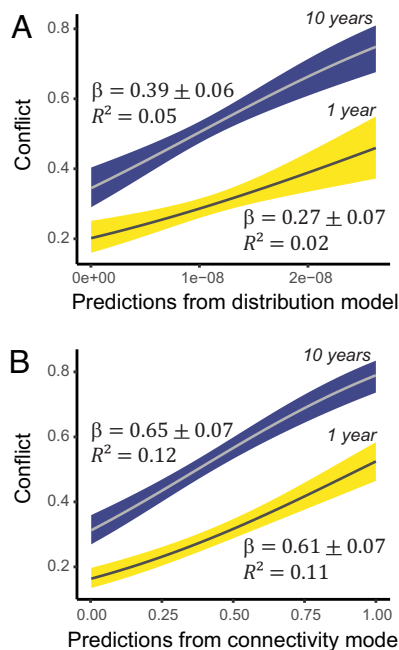


Fig. 4. The predicted probability of conflict over 1 y (shaded yellow), and over 10 y (shaded blue), based on (A) a distribution-based model (used for creating resistance and conflict maps; *SI Appendix, Fig S2*) and (B) time-specific predictions from the connectivity model. Overall, the connectivity model fit the data better than the distribution-based model as per model-selection criteria, had greater effect sizes (based on beta estimates from scaled metrics), and explained 2.5 to 5 times the variation based on pseudo- R^2 values.

We note that the same may not hold if conflict mortality increases. Nonetheless, even for the rates of conflict we used, conflict-induced mortality impacted movement, and we found that even lesser intensities of predicted or manifested conflict could result in blocking connectivity in some locations (*SI Appendix, Fig. S4*). Small increments in conflict-induced mortality can also necessitate large amounts of conflict-free habitat for long-term population viability of species (32), a luxury that conservation landscapes in the densely populated tropics seldom possess.

Second, conservation strategies directed at each source of mortality may be different. Hence, decomposing the different sources of mortality can help prioritize conservation strategies and address trade-offs among them (38, 39). For instance, addressing conflict mortality may entail: a) stringently restricting removal of elephants by managers; b) enhanced stakeholder engagement to minimize retaliatory killings; and c) transparent compensation to mitigate financial and other losses to farmers due to elephants.

Third, predicted mortality arising from conflict shows distinct spatial patterns in comparison with natural mortality, allowing us to distinguish secure corridors from the connectivity–conflict interface (Fig. 1). This is best highlighted in Fig. 2B, where we map spatial patterns of conflict, predicted by the SAMC model, with net visitation rates (movement paths), highlighting where these collide. This can also be visualized in *SI Appendix, Fig. S4B*, where we depict the loss of movement paths between protected areas (loss in net visitation rates) from conflict. The impact of conflict on connectivity depends on the location, such that, even low intensities of conflict along movement paths can severely lower connectivity, as compared with elsewhere. Contextualizing these spatial patterns requires modeling conflict and connectivity simultaneously. Similar issues occur for mortality risks arising from causes such as roads (40), human disturbance (17), or vegetation characteristics across the landscape (23). These too may require different conservation strategies such as overpasses and other

mitigation for linear infrastructure or restoration to modify vegetation structure to reduce mortality risk.

Importantly, spatial conflict patterns have social-ecological underpinnings. In our region, for example, croplands had high levels of conditional conflict (given elephant use of the matrix) compared with agroforests and human settlements. Crop depredation is a primary driver of human–elephant conflict (7), and it is likely that elephant use of croplands spurred a strong response from people to protect against crop loss. In contrast, with a relatively low risk of financial loss in settlements and agroforests, people likely safely avoided elephants. Human responses and underlying attitudes toward wildlife can therefore show variation across space and can strongly shape movement patterns and connectivity across conservation landscapes (11, 18). Conservation strategies can follow this pattern, focusing on reducing crop depredation through different means (reviewed in ref. 10) while working closely with stakeholders to ensure continual safe passage of elephants in agroforests and human settlements. Explicitly tracking multiple causes of dispersal failure while accounting for landscape resistance to animal movement addresses a critical need to link landscape conservation prioritization to animal behavior and movement theory (13, 41). Since human–wildlife conflict varies in space and time (7), there is need for landscape-scale conservation and planning for connectivity to be adaptive and dynamic (42). There have been models that look more deeply into source-sink dynamics to assess spatial impacts of human disturbance (21). Our model would benefit from information on population demography, including accurate estimates of emigration from each population; nonetheless, it provides fine-scale spatial information on predicted conflict mortality across the landscape, juxtaposed with spatial information on animal corridors.

The implications of conflict for animal mortality, both due to retaliatory killing, as well as lethal control and removal (8), are substantial. In the specific context of Asian elephants in India, conflict-induced mortality can arise from electrocution, poisoning, traps and bombs, or direct retaliatory killing (27). An estimated 100 elephants die annually from conflict in India (response in parliament by the Minister of Environment, Forest and Climate Change, Govt. of India; August 2, 2021), though this number is likely an underestimate. Conflict is intense in the state of Karnataka where we map the connectivity–conflict interface: it has among the highest number of reported wildlife conflicts across India and the government spends around USD 1.5 million annually in compensatory payments for conflict, primarily with elephants (28, 43). Capture of “problem animals,” a method that was widely used historically but strictly regulated in more recent decades due to its ethical underpinnings (20), is now receiving attention as a potential conflict mitigation measure. Indeed, “dangerous” animals moving through human spaces are captured or killed across taxa and geographies (6, 44). Our results provide insight in light of these lethal responses to conflict.

Conservation Applications. Our framework can provide guidance in identifying context-specific conservation actions, even in situations where conflict may not lead to mortality. We argue that spatial locations in conservation landscapes generally fall into one of four categories based on connectivity and conflict (Fig. 2B). Of these categories, locations of least conservation concern are those that play little or no role in connectivity and face minimal conflict; conservation strategies in these locations can be focused on increasing animal movement through habitat restoration, increasing woody vegetation or encouraging land uses that facilitate connectivity (16, 45). Lands that allow connectivity and face minimal conflict have the highest potential for long-term conservation and human–wildlife

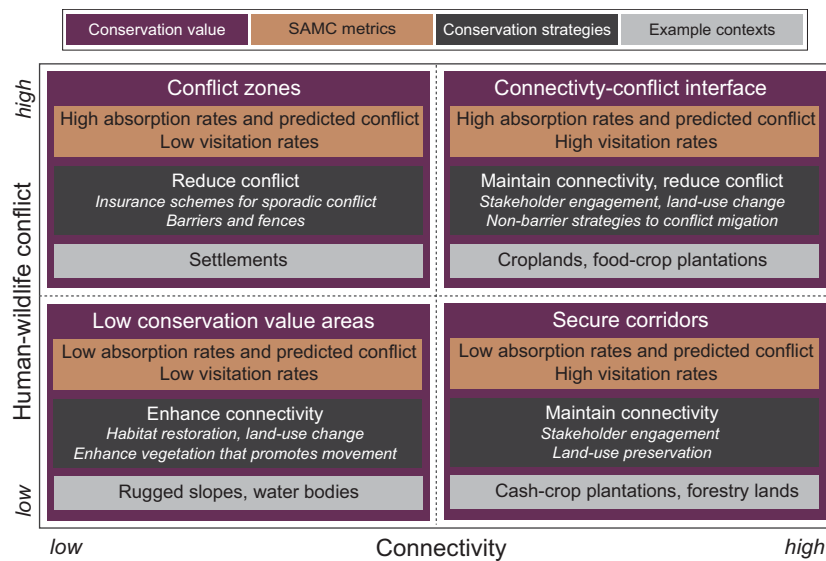


Fig. 5. Locations across conservation landscapes can be categorized into one of four scenarios of conservation value and focus, based on their contribution to connectivity—arising from their movement permeability and location (*SI Appendix, Fig. S2A*)—and conflict intensity given elephant use, measured as visitation rates and absorption, respectively, in the SAMC model. Each quadrant relates to different SAMC parameters and output and call for a different set of conservation strategies. We provide example land uses from our study context for each quadrant. Predicted conflict (Fig. 2) will be high at the connectivity–conflict interface; it is likely to be sporadic in conflict zones that have low visitation rates but high absorption rates.

coexistence; conservation efforts here need to be tuned toward maintaining status quo.

Our approach enables identification of hotspots of conflict that are frequented by wildlife (high visitation rates) to be distinguished from those locations that are visited with low frequency (low visitation rates) (Fig. 2*B*). Conflict mitigation in these two contexts needs to be different. In conflict hotspots with low visitation rates, conflict is likely to be sporadic and may thus be suitable for insurance schemes (46), or strategies aimed at restricting animal entry through barriers (e.g., fences). Conflict hotspots with high visitation rates, or the connectivity–conflict interface, require strategies that can address conflict while simultaneously allowing continued animal movement; where conflict cannot be mitigated, redirecting movement to alternative corridors to reduce negative human–wildlife interactions could be a viable strategy.

In the context of the Mysore ER, our findings suggest careful evaluation and potential realignment of current management strategies to better balance this dual conservation need in the connectivity–conflict interface. We illustrate our argument for a shift in on-ground conservation practice with the help of two examples. First, the government is investing between USD 6,000 to 200,000/km on fences as a conflict mitigation strategy in this landscape (47). Among other areas, these fences have been installed along the northern boundaries of Nagarhole and Bandipur, two contiguous protected areas that support key populations of elephants (*SI Appendix, Fig. S1*). By separating the two protected areas from the connectivity–conflict interface, the fences can potentially mitigate conflict, but at the cost of elephant dispersal through the landscape (Fig. 2*B* and *SI Appendix, Fig. S5*); anecdotal media reports also indicate mortality risk to individual elephants trying to circumvent these fences. Thus, our analysis suggests that the fences are an unbalanced conservation solution, and it offers insights into where these conservation costs are better invested. Second, to mitigate conflict, the government captured and removed 22 elephants from the Alur-Sakleshpur area of the landscape (*SI Appendix, Fig. S5*) in 2014 because the area was considered to house an isolated elephant population of c. 30 animals in a nonhabitat matrix dominated by agroforests (48). In

contrast, our results predict agroforests in the landscape, including the Alur-Sakleshpur area, to have moderate–high net visitation rates and low–moderate conflict levels (*SI Appendix, Fig. S5*), thereby highlighting their potential to serve as secure corridors (Fig. 5). The fact that the Alur-Sakleshpur area was recolonized by elephants within a year of the removal operation (48), suggests that it was never an isolated population, corroborating our current findings. Our results provide scientific support for the expected and observed recolonization, and results indicate that reactive removal of elephants from Alur-Sakleshpur (or potentially other fragmented habitats) may not be effective.

More broadly, our results suggest that assessment and implementation of conflict mitigation strategies should be tailored to the connectivity–conflict interface (Fig. 5). At the interface, mitigation strategies need to be long-term, involving stakeholder engagement, land-use planning, and community-based interventions that are free of barriers or rely on them only for localized crop protection without impeding movement through the landscape (Fig. 5). We found that high-conflict locations also overlapped with locations that were resistant to movement, compounding barrier effects on connectivity, which may decrease the extent of the connectivity–conflict interface. In other landscape contexts, however, conflict and movement permeability may be uncorrelated (23, 44), expanding the scope of the connectivity–conflict interface. Mapping the connectivity–conflict interface can sharpen conservation strategies and enable them to be locally designed toward mitigating conflict without leading to a loss of connectivity.

Materials and Methods

The SAMC Framework. The SAMC framework captures processes of movement and absorption (i.e., the termination of movement from mortality, settlement, or related processes) through the construction of a probability matrix, $\mathbf{P}$, that contains both transition probabilities between transient states (e.g., patches or landscape cells) and one or more absorbing states. For a landscape divided into C cells or patches, matrix $\mathbf{P}$ can be written as:

$$\begin{pmatrix} \mathbf{Q} & \mathbf{R} \\ \mathbf{0} & \mathbf{1} \end{pmatrix}, \quad [1]$$

where $\mathbf{Q}$ is a $C \times C$ transition matrix reflecting transitions between transient states, $\mathbf{R}$ is a $C \times 1$ vector containing transition probabilities from the transient states to the absorbing state, and $\mathbf{0}$ is a $1 \times C$ vector of zeros. The elements p_{ij} describe the probability of transitioning from state i to j in one time step.

We extend this model to include multiple absorbing states. Here, we show how two different absorbing states can be considered: one reflecting natural causes of mortality and a second reflecting absorption due to removal from human-wildlife conflict. Our new $\mathbf{P}$ matrix can be described as:

$$\begin{pmatrix} \mathbf{Q} & \mathbf{R}_m & \mathbf{R}_c \\ \mathbf{0} & 1 & 0 \\ \mathbf{0} & 0 & 1 \end{pmatrix}, \quad [2]$$

which is a $(C+2) \times (C+2)$ transition matrix, where $\mathbf{R}_m$ contains the absorption probabilities reflecting natural causes of mortality, and $\mathbf{R}_c$ contains the absorption probabilities reflecting removal due to human-wildlife conflict. For each row, $\sum_{j=1}^{C+2} p_{ij} = 1$. Consequently, this extension allows the decomposition of different types of absorption on movement and connectivity across landscapes.

With this matrix, we can map the long-term (asymptotic) probability of conflict at location j if starting in location i as the (i, j) th element of $\mathbf{B}$,

$$\mathbf{B} = \mathbf{F}\tilde{\mathbf{R}}_c, \quad [3]$$

where $\mathbf{F} = (\mathbf{I} - \mathbf{Q})^{-1}$ (aka the "fundamental matrix"), $\mathbf{I}$ is an identity matrix, and $\tilde{\mathbf{R}}_c$ is a $C \times C$ matrix with diagonal elements equal to $\mathbf{R}_c$ and off-diagonal elements equal to $\mathbf{Q}(23)$.

We also calculated time-specific conflict predictions. The probability of experiencing conflict at location j within t or fewer steps if starting in location i is the (i, j) th element of the matrix,

$$\mathbf{B}_t = \left(\sum_{n=0}^{t-1} \mathbf{Q}^n \right) \tilde{\mathbf{R}}_c = (\mathbf{I} - \mathbf{Q})^{-1} (\mathbf{I} - \mathbf{Q}^t) \tilde{\mathbf{R}}_c. \quad [4]$$

We incorporate variation in population size of elephants in protected areas as:

$$\Psi^T \mathbf{B}, \quad [5]$$

where Ψ is a vector of relative abundances of length C for relative abundance across the landscape and $\mathbf{T}$ is the transpose of this vector.

Finally, we mapped the predicted movement and flow of elephants based under assumptions of no constraints regarding absorption from natural mortality or conflict relative to expectations of flow under human-elephant conflict. To do so, we calculated net visitation rates over space (34). Visitation rates are the (i, j) th element of $\mathbf{F}$, which describe the total time a disperser spends at location j if starting in location i . The net visitation rates describe the net movement probabilities between k and l if starting in location i , which are proportional to the difference in time spent at a location times the transient transition probabilities:

$$l_{kl} \propto \text{abs} (f_{ik} q_{kl} - f_{il} q_{lk}), \quad [6]$$

where f_{ij} and q_{ij} are elements of the matrices $\mathbf{F}$ and $\mathbf{Q}$ (34). This metric is identical to the mapping of "current density" as accomplished with circuit theory (30) when no absorption occurs. We scaled this metric to elephant population size in each of the five protected areas, our key populations, as:

$$l_{kl} \propto \text{abs} (\psi_i f_{ik} q_{kl} - \psi_i f_{il} q_{lk}), \quad [7]$$

where ψ_i is the population size of elephants for key population i . Consequently, net visitation rates in this context describe the expected net movement rates of individuals. We compared this idealized situation with the expectation for human-elephant conflict to impede movement across the landscape.

Parameterizing the SAMC Model. We parameterized the SAMC model in the following way. First, we resampled 30×30 -m land cover to a 500×500 -m resolution for mapping. We used this resolution to reflect average hourly movement of elephants, based on GPS-telemetry that shows average elephant movement of 0.35 to 0.52 km per h across different land uses (49–51); thus, we assume a time step in the Markov chain reflects approximately 1 h.

We then created a resistance layer based on the inverse of estimates of occupancy (derived from survey data as described in the section below) by the proportion of each land-cover type within each 500×500 -m cell (habitation, plantation,

open crop, water, other plantation, forest) and human population density to parameterize $\mathbf{Q}$. We excluded habitation because it was redundant with human population density. Exploratory analyses showed no effect of the proportion of water on occupancy or conflict, so we removed that land-cover covariate from models. For our estimates, we clamped estimated effects across the landscape based on the observed data used in the occupancy model, as described below.

Empirical Data for Modeling Connectivity and Conflict. To guide our field survey and ensure spatial coverage, we mapped a 6-km buffer around Nagarhole, Bandipur and Bhadra, and overlaid a network of 3.6-km grid cells over this buffer. This provided us with a combined network of 182 grid cells around Nagarhole and Bandipur (Nagarhole: 84, Bandipur: 98), spanning an area of 2,366 km²; and 113 grid cells around Bhadra, spanning an area of 1,469 km². We used Quantum Geographic Information System (QGIS) v. 2.18.26 for GIS-related analyses.

We interviewed respondents, mainly farmers, in our grid network to record information on elephant use of the area and the incidence of conflict. Interviews were conducted by trained teams in the local language, Kannada. Our interview and survey methodology were reviewed and approved by the institutional ethics committee for research on human subjects of the Centre for Wildlife Studies. All surveys were carried out by trained teams and were preceded by a plain language statement in the local language Kannada, describing the survey objectives, and policy of anonymity. Consent was obtained orally from respondents before initiating the survey. Respondents within each grid cell were chosen opportunistically and separated spatially by distance intervals of at least 700 m to ensure independence of responses and adequate spatial coverage of each grid cell. We interviewed four to six respondents within each grid cell. We focused on grid cells with agriculture, plantations, and habitation; grid cells with complete forest cover, mountainous terrain, and those without any habitation or agriculture were excluded from our survey, as these cells lacked respondents to report elephant use, nor were they prone to conflict.

We used structured questionnaires, recording in each survey whether respondents had noted elephant presence in their neighborhood in the previous month. Wherever possible, we validated the presence of elephants by documenting signs such as footprints or dung. We also recorded if the respondents had faced conflict, in the form of crop loss, property damage, or human injury and loss of life. We surveyed the landscape for six time periods to capture seasonal conflict or elephant use of the landscape, on a bimonthly basis, covering in total a period of a year between January and December 2017. Respondents across surveys were independent of each other.

Parameterizing Resistance and Conflict Intensity. We used logistic regression to test the effect of land use and human density on a) elephant use of the multi-use landscape, and b) probability of conflict, conditional on elephant use ("conditional conflict"). We recorded land use information from our field surveys and categorized the following land cover types: i) human habitation, ii) agroforest (primarily coffee, rubber, and mixed plantations), iii) cropland (including all open food crops and some cash crops like tobacco), iv) water body, v) open plantation (coconut and areca nut) and vi) forest, with a resolution of 250 m and an overall classification accuracy of 0.89 and a κ statistic of 0.81. We collated information on pixel-level human population density, adjusted to match UN-population estimates, from the Worldpop database v. 2.0 (from www.worldpop.org) for the year 2015. We considered both untransformed values and a log-transformed measure of human population size. We tested additive and interactive effects of land cover and population density, and selected the best-supported model using the Akaike's Information Criterion.

To assign pixel-wise land use classes to the Mysore ER, we obtained Landsat 8 OLI/TIRS Level-2 multispectral satellite images with 30-m resolution, for the period of March to April 2017, for cloud-free images. We used 27 polygons of each of the classes as training data, obtained from photo interpretation of satellite imagery and the 11,762 ground-truth points recorded during field surveys. We used a supervised classification approach using a spectral angle mapping algorithm within the semi-automatic classification plugin on QGIS. We then extracted the modal, or most represented, land use in a 250-m pixel. We used this information, in combination with human population density, as obtained from the WorldPop database, to predict resistance (from the inverse of probability of elephant use of the landscape), and probability of conflict, conditional on elephant use, from the models described above. We scaled the resistance values to appropriately

represent heterogeneity in the landscape and set a ceiling value of 500 to ensure model convergence. In our landscape, there were estimates of human density (urban environments) in the region that were greater than what we observed in the data used for model building. Clamping, or setting a ceiling value of predicted resistance, resulted in predictions that assumed that these more urban settings would have similar effects on movement/connectivity as the most urban areas we used in model building. This approach has frequently been used to bound predictions in distribution modeling (e.g., ref. 52). We treated the probability of conditional conflict as a proxy for conflict-induced mortality and assigned spatially informed pixel-specific indices of conflict probability across the Mysore ER. We scaled probabilities such that baseline mortality, and conflict-induced mortality of elephants matched realistic values (32).

To parameterize R_{nr} , or absorption arising from natural (nonconflict) mortality, we assumed a constant probability of mortality per time step derived from annual estimates of survival of Asian elephants of 0.97 (32). To parameterize R_c , or absorption arising from conflict-driven mortality, we estimated expected conflict, given elephant use in the following manner. We first fit a logistic regression model based on locations where conflict was observed during field surveys using the proportion of land cover and human population density, conditional on elephant presence being reported from surveys. As land cover effects on conflict may be contingent on human population density, we considered pairwise interactive effects in this model in addition to additive effects. Based on the most supported model, we then scaled the odds from this model to observed variation in conflict reported previously from the ER as the number of incidences of conflict per 100 km² per year (27). We converted the minimum (1) and maximum (893) number of incidences to probabilities per pixel per time step using the relationship of the Poisson distribution with the complementary log-log link function. Given an area A and a location i , we assume the number of reported incidences N_i follows a Poisson distribution as:

$$N_i \approx \text{Pois} (A_i \exp(\alpha)), \quad [8]$$

where α is the estimated number per unit area on the log link scale. The probability of a conflict incidence given elephant use can be derived using the complementary log-log link function:

$$\Pr(N_i > 0) = 1 - \exp(-\exp(\alpha + \log A_i)). \quad [9]$$

As such reported incidences implicitly reflect an unknown density of elephants moving through the region, we also conducted a sensitivity analysis on model predictions based on varying both assumed annual mortality (0 to 0.06; 32) and conflict rates. Overall, spatial patterns were similar to predictions shown here.

Finally, for abundances, we used empirical density estimates from the region (53, 54). We scaled densities to the perimeter of each protected area, such that dispersers started at the boundary of protected areas and the relative numbers of dispersers were proportional to the density of elephants in the protected area. This model was implemented with the *samc* package in R (55), which we extended to allow for multiple absorption states.

Model Validation. We used two sources of data for model validation. First, we collated reports of human–elephant conflict from a semi-structured questionnaire survey in the study region that occurred between April and December 2017, as part of a larger effort to assess the use and perceived efficacy of conflict mitigation measures for different crop types. We also included a 6-km buffer around an additional protected area, the Biligiri Ranganatha Swamy Temple

Tiger Reserve (henceforth, Biligiri). The field team recorded information from respondents on agricultural practices, specifically, on crops grown, and conflict incidents faced. We thus obtained data on spatial locations where conflict did and did not occur.

Second, we collected reports on human–elephant conflict reported in the media (e.g., newspapers) in the state of Karnataka for a 36-mo period between 2013 and 2015. We included newspapers in both English and Kannada (the regional language in our study area) and used systematic online searches to record any instances of conflict. Multiple reports of a single incident of conflict across different papers were collapsed into a single datapoint. Each reported incident was spatially referenced to the involved village or location. We considered these data as “presence-only” data and contrasted model predictions at observed locations to 10,000 available locations across the landscape.

We used two evaluation metrics: the area under the ROC Curve (AUC), and the True Skill Statistic (TSS). We also report the ratio of the average predictions at observed conflict sites to the average predictions for nonconflict (for questionnaire data) or background sites (for media reports). The use of TSS requires setting a threshold for model predictions. As predicted values of conflict were small for any pixel on the landscape, we used the mean predicted value as a threshold. It is generally recommended to consider multiple metrics for comprehensive model evaluations to reflect different kinds of summaries of model discrimination. The AUC (range: 0 to 1) and TSS (range: −1 to +1) statistics that we use are two of the more common metrics (56). All evaluation metrics were calculated with the PresenceAbsence package (57).

Finally, we also contrasted model fit and predictions from the connectivity models with those from distribution-based models for resistance and conflict (SI Appendix, Fig. S2 and Tables S3 and S4) to understand whether an explicit connectivity model was necessary for conflict predictions. For the distribution-based model, we calculated the joint probability of conflict as the product of elephant occupancy and conditional conflict (models shown in SI Appendix, Tables S2–S4). The difference in the connectivity-based and distribution-based models lies in the capturing of the explicit movement process into conflict predictions in the SAMC.

Data, Materials, and Software Availability. Data on elephant and conflict locations, validation points, and code used in analysis data are deposited at Figshare (<https://doi.org/10.6084/m9.figshare.20227503>) (58).

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