RESEARCH ARTICLE

Identifying important connectivity areas for the wide-ranging Asian elephant across conservation landscapes of Northeast India

Divya Vasudev[1,2,3] [ID] | Varun R. Goswami[1,2] [ID] | Nishanth Srinivas[1] |
Biang La Nam Syiem[1,2,4] [ID] | Aishanya Sarma[1]

[1]Conservation Initiatives, Guwahati, Assam, India

[2]Centre for Wildlife Studies, Bengaluru, Karnataka, India

[3]Wildlife Conservation Trust, Mumbai, Maharashtra, India

[4]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Melbourne, VIC, Australia

Correspondence
Varun R. Goswami, Conservation Initiatives, Six Mile, Guwahati 781022, Assam, India.
Email: varunr.goswami@gmail.com

Abstract

Aim: Connectivity is increasingly important for landscape-scale conservation programmes. Yet there are obstacles to developing reliable connectivity maps, including paucity of data on animal use of the non-habitat matrix. Our aim was to identify important connectivity areas for the endangered Asian elephant *Elephas maximus* across a 21,210 km^2 region using empirical data and recently developed animal movement models.

Location: Northeast India.

Methods: We interviewed 1,184 respondents, primarily farmers, residing across our study region, to collect crowd-sourced data on elephant use of the matrix. We generated a classified land use/land cover map and collated remotely sensed data on environmental and anthropogenic covariates. We used logistic regression to estimate the influence of these covariates on resistance, based on elephant detections recorded via interviews. We modelled elephant movement within the randomised shortest path framework, which allows for scenarios ranging from optimal movement with complete information on the landscape to random movement with no information on the landscape. We calculated the passage of elephants through pixels in our study region, a parameter that denotes the expected number of elephant movements through a particular pixel across movement routes. We overlaid linear infrastructure sourced from secondary data, and human–elephant conflict hotspots generated from our interview data, on passage maps.

Results: Elephants preferred locations with high vegetation cover, close to forests and with low human population density. We mapped important connectivity areas across the study region, including in three important conservation landscapes. Whilst forests facilitated connectivity, the matrix also played an important contributory role to elephant dispersal. Incorporating information on environmental and anthropogenic drivers of elephant movement added value to connectivity predictions.

Main conclusions: Fine-scale mapping of connectivity, using empirical data and realistic movement models, such as the approach we use, can provide for informed and more effective landscape-scale conservation.

KEYWORDS

Assam, corridor, crowd-sourced data, dispersal, forests, fragmentation, linear infrastructure, movement models, randomised shortest path, resistance mapping

1 | INTRODUCTION

Connectivity, or functional linkages between populations or resource patches (Vasudev, Fletcher, et al., 2015), is crucial for maintaining species viability and ecosystem functioning, particularly in the light of ongoing environmental change (Doerr et al., 2011; Staddon et al., 2010). Connectivity, forged by dispersal of individuals across populations or habitats (Clobert et al., 2012), determines where species are (Peterson et al., 2011), as well as their ability to adapt to novel environments (Holderegger & Wagner, 2008) and climate change (Parmesan & Yohe, 2003). Connectivity shapes inter-species interactions such as competition, predation and seed dispersal, ultimately influencing ecosystem health and function (Orrock et al., 2006; Staddon et al., 2010). Thus, maintaining connectivity is a critical need for landscape-scale conservation programmes.

However, animal movement is severely restricted in the Anthropocene (Tucker et al., 2018). Furthermore, evidence across taxa and landscapes demonstrates the negative impacts of reduced connectivity on species and communities (Fletcher et al., 2016). Connectivity is potentially impeded by a number of factors, including linear infrastructure such as roads and rails (van der Ree et al., 2015), land uses through which animal movement is restricted, or where dispersing animals face heightened risk, and human habitation (e.g. Kramer-Schadt et al., 2004; Thatte et al., 2018). Antagonistic responses of people to dispersing animals, such as chasing of "conflict" animals, and certain mitigation measures for human–wildlife conflict, such as fences, can also pose a barrier to connectivity (Ghoddousi et al., 2021; Goswami & Vasudev, 2017; Laundré et al., 2001). Yet, for most species, we have little quantitative knowledge of the impacts of these barriers to connectivity (but see Fletcher et al., 2019; Osipova et al., 2018); this, in turn, means we are limited in our ability to successfully achieve connectivity conservation targets (Vasudev, Fletcher, et al., 2015). Clearly, we need a better understanding of animal movement across heterogeneous landscapes, and more accurate modelling of connectivity to develop effective connectivity conservation strategies and targeted interventions (e.g. overpasses to mitigate impediments due to linear infrastructure).

Connectivity is shaped by intrinsic characteristics of species, the external environment, and the spatial configuration of landscape elements (Nathan et al., 2008; Vasudev, Fletcher, et al., 2015). Interactions between dispersing animals and the environment determine the *resistance* of the matrix—non-habitat sections of the landscape—to the animal movement (Taylor et al., 1993). Thus, certain landscape elements, such as rivers or roads, can pose *barriers* to connectivity, whilst others, such as woodlands may serve as *corridors* for animal movement. More recently, barriers and corridors have been seen as two sides of the same coin, representing a continuum of the role that different areas play in facilitating (or impeding) landscape connectivity (Panzacchi et al., 2016).

Whilst the concept of matrix resistance is increasingly incorporated into connectivity modelling (Fletcher et al., 2016), parameterising resistance-based models remains a non-trivial issue (Panzacchi et al., 2016; Zeller et al., 2012). Observations of the large-scale and infrequent movement events that typically comprise species dispersal have become more feasible with the advent of telemetry (Hooten et al., 2017). Nevertheless, telemetry remains inapplicable to a large number of species and regions due to high costs and logistical constraints, factors that often also limit sample sizes in those studies that do incorporate the approach. Thus, resistances are often parameterised through expert opinion or proxies, typically invalidated by field information on animal use of the matrix (Sawyer et al., 2011; Zeller et al., 2012). An alternative option for easily detectable species such as birds or large non-elusive mammals is crowd-sourced or citizen-science data (Brown et al., 2018; Frigerio et al., 2018). Such information is useful as it allows researchers to cover large landscapes and temporal scales adequate to attain sufficient sample sizes of infrequent dispersal events. The Asian elephant *Elephas maximus* is one such non-elusive, detectable and easily identifiable wide-ranging species, for which connectivity is a critical conservation need (Goswami & Vasudev, 2017; Goswami et al., 2021).

The suite of available connectivity models that can incorporate matrix resistances represents two ends of a spectrum. At one end are least-cost models, which assume that dispersers move optimally, with complete knowledge of the landscape (Adriaensen et al., 2003). At the other end are random-walk models, such as those based on circuit theory, which assume that dispersers have information solely on their immediate environment (McRae et al., 2008). One advantage of the latter has been its ability to account for path redundancy, thereby providing a more accurate representation of landscape connectivity (McRae et al., 2008). The likely reality though is one that lies somewhere between the two extremes, whereby dispersing animals attempt some degree of non-optimal exploration of the landscape, have some knowledge about their surrounding landscape, and make movement decisions accordingly. The randomised shortest path (RSP) framework offers this balance, explicitly incorporating an *information* parameter θ, which controls the trade-off between random exploration of the

landscape by dispersers, and optimisation of movement (Kivimäki et al., 2014; Panzacchi et al., 2016). In so doing, the RSP framework offers a modelling approach that can more realistically represent animal movement across heterogeneous landscapes (Panzacchi et al., 2016).

We use the RSP framework in combination with crowd-sourced data to prioritise important connectivity areas for the wide-ranging Asian elephant across a large region in Northeast India. We estimated resistances using crowd-sourced information, systematically collected via a questionnaire survey. We then modelled animal movement across the region using the RSP framework. We parameterised the movement model using estimated resistances and modelled multiple scenarios of disperser information on their environment. We compared movement models parameterised solely by land use, and those that incorporated more detailed information on the landscape. Finally, we overlaid two types of threats to connectivity on modelled animal movement: (a) linear infrastructure, including roads and railways, and (b) human–elephant conflict hotspots, as recorded from our surveys. We discuss the relevance of our findings for landscape-scale conservation of this endangered species.

2 | METHODS

2.1 | Study area

Our study area encompassed a large 21,210 km^2 region in the foothill plains of central Northeast India (Figure 1a). The region lies on the southern bank of the Brahmaputra River in the state of Assam and includes an adjoining northern portion of the state of Meghalaya. Two important Elephant Reserves (ERs) are situated fully, or in part, in our study region, namely, the 3,270-km^2 Kaziranga–Karbi Anglong ER inhabited by an estimated 1,746 elephants at the minimum (Goswami et al., 2019), and the 2,740 km^2 Dhansiri–Lumding ER (which includes the Kholahat Reserve Forests) home to an estimated 205 elephants (Rangarajan et al., 2010). Elephant Reserves in India are important elephant conservation landscapes, comprising protected areas (e.g. protected National Parks or Wildlife Sanctuaries), other forests with lower degrees of protection (e.g. Reserved Forests), and other non-protected lands (e.g. agricultural fields, plantations). ERs are declared in recognition of the need for landscape-scale conservation efforts for the wide-ranging Asian elephant. ERs are not fenced, but individual private lands, or forests within ERs, may have fences along their respective boundaries. Our study region also includes the forests in Garo Hills, Meghalaya, and the Rani landscape of Assam, which are elephant conservation areas of known importance. The region receives an average rainfall of about 1,500 mm annually, with the monsoon season (June–September) accounting for most of the rain. The grasslands, moist evergreen forests and deciduous forests that form elephant habitat in this region are fragmented. These elephant habitats are surrounded by a matrix comprising mostly of rice paddy *Oryza sativa* fields, tea *Camellia sinensis* and sal *Shorea robusta* plantations, and human habitations (Figure 1a). Rice paddy fields are open lands with few to no trees, and they are often small landholdings and unfenced. Tea plantations, depending on management of the plantation, may offer varying

degrees of tree cover, and maybe fenced with bamboo, wire, or solar fences. Dispersing elephants traverse this matrix to access resources and refuge (e.g. Goswami et al., 2021). It was this matrix that thus formed the primary focal area of our study.

2.2 | Field survey

Our aim was to sample large parts of our study region, which has high human population density, to assess elephant use—however infrequent—of the matrix. For a detectable and identifiable species like the elephant, we decided to use crowd-sourced information, systematically collected via a questionnaire survey, so as to sample a large area at a relatively fine scale, whilst obtaining adequate reports on elephant use of the matrix.

To sample the region in a systematic fashion and attain adequate spatial coverage, we divided the geographical extent of our study area into a grid network of 286 cells, each of size 25-km^2. Thus, our sampled grid effectively covered an area of 7,150 km^2. This grid was not used for analyses, but guided our sampling such that we achieved spatial spread and even coverage of our entire sampled area, thereby minimising any potential sampling bias. For our assessment of resistance, we restricted ourselves to respondents from Assam, as the social-ecological context of this state and the neighbouring state of Meghalaya are quite different. Assam also comprised most of our study region and housed the majority of our respondents. We overlaid a buffer of width 10-km around survey locations, resulting in our total study area of 21,210 km^2 (Figure 1a). We chose a buffer of 10 km, as it is comparable to elephant home range and space-use radii reported in previous studies (Goswami, Vasudev, et al., 2014; Goswami et al., 2019). Our survey was part of a larger effort to obtain information relevant to landscape-scale elephant conservation in Northeast India.

We systematically interviewed respondents, primarily farmers, from the survey area between June 2019 and March 2020. We used the grid network as a spatial guide, and interviewed 4–8 respondents per cell, chosen opportunistically. Interviews were conducted at locations separated by at least 400 m, to ensure the independence of responses and adequate spatial coverage within grid cells. As a further precaution against pseudo-replication, we confined our analysis to a subset of respondents who were separated by 1 km or more, aligning with our resolution of analysis. Each respondent represented a sample point in our analysis.

The questionnaire surveys were conducted by trained field teams in the local languages, after obtaining consent from respondents. We undertook a structured interview, instrumented using the Open Data Kit (Hartung et al., 2010). We questioned each respondent on elephant presence over the past year within their neighbourhood, which we defined as a buffer of 1 km around the respondent. Where possible, we validated the presence of elephants by documenting signs such as footprints or dung at the exact sites of movement. If a respondent sighted elephants multiple times in a year, we collapsed these into a single sighting to represent whether the sampled location was used, or not, by elephants. A note on the presence of captive elephants was
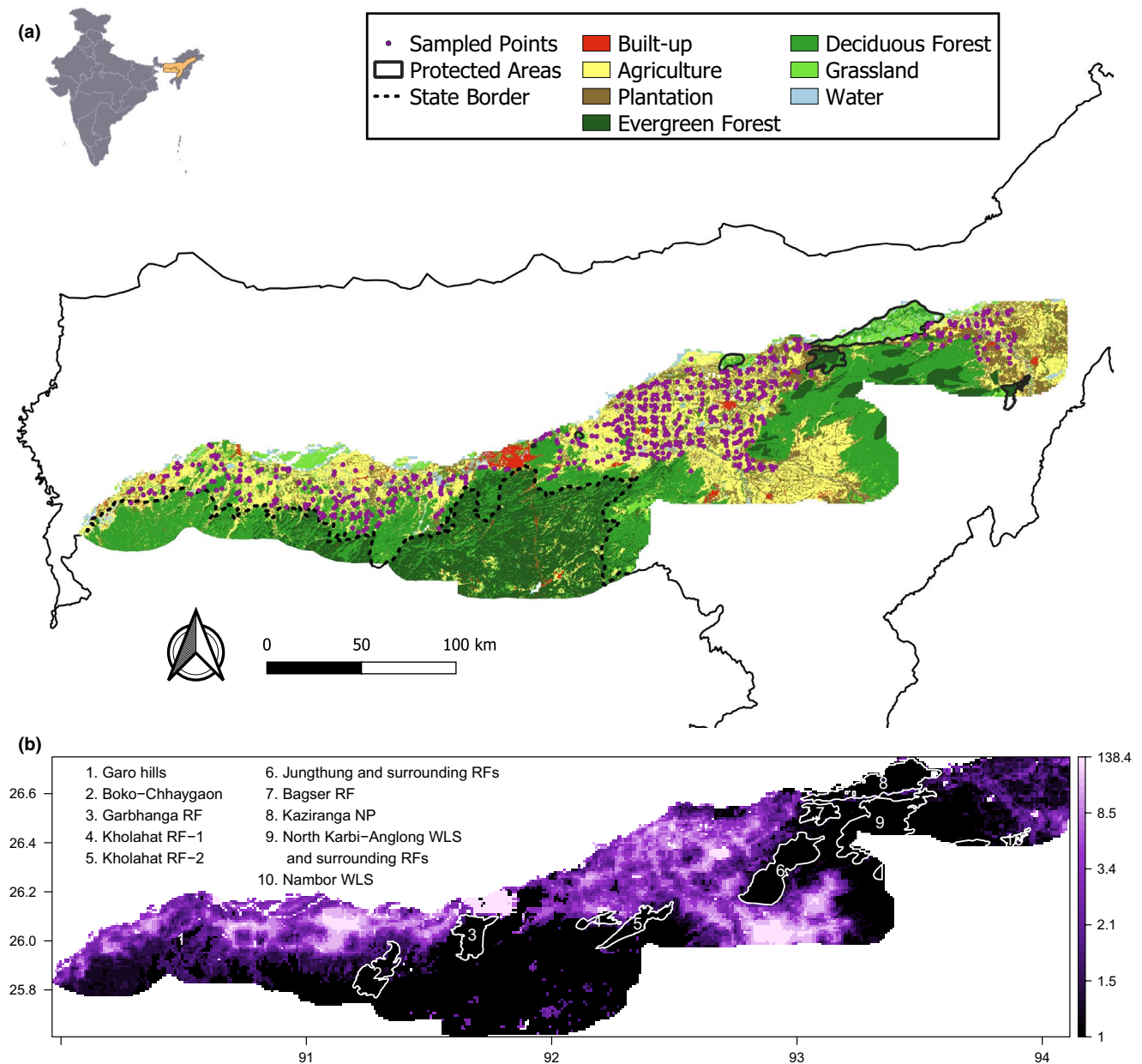
FIGURE 1 (a) Map of the study region showing survey points and classified land use/land cover. The inset shows the location of the study region in India. (b) Model-averaged estimated resistance to movement across our study region. We also show 10 identified source populations in the study region (white, numbered polygons; RF: Reserved Forest, NP: National Park, WLS: Wildlife Sanctuary)

also kept, so as to not mistake these elephants as those from wild populations. We recorded local land use, which we used for ground-truthing land use/land cover classification, described further below. Lastly, we asked respondents if they faced conflict with elephants, in the form of crop loss, property damage, human injury or loss of life.

2.3 | Modelling elephant space use

We assessed the influence of environmental and anthropogenic variables on the probability of elephants using sampled locations in the

landscape, that is, locations corresponding to the field questionnaire survey described above. This provided us with a basis to parameterise landscape resistance (see Section 2.4). Each sampled location was associated with information on whether respondents had detected elephants or not, during the past year. We additionally extracted a set of ecologically relevant covariates, as described below, within a 1-km^2 square window centred around each point location; this buffer aligned with the dimensions of the elephant detection data, as well as with our final predicted resistance maps.

We used the following remotely sensed covariates. We derived the Enhanced Vegetation Index (Huete et al., 2002) which represents

vegetation cover, or greenness of locations, at a 20-m resolution, using Sentinel-2 Multi-Spectral Instrument Level-2A images of resolution 10 m to 60 m (Drusch et al., 2012; Gorelick et al., 2017) from the Google Earth Engine (Gorelick et al., 2017). The data covered the period Feb 2019 to Jan 2020, which largely overlapped with our field survey period, and had a revisit time of 5 days. We excluded imagery with greater than 10% cloud cover from the resultant single median composite image. We aggregated the derived EVI data to a resolution of 1 km using the zonal statistics function of Google Earth Engine. We obtained information on elevation and slope from Advanced Land Observing Satellite ALOS World 3D – 30 m Version 3.1, a global digital surface model dataset (Tadono et al., 2016). We extracted spatial data on human population density from the WorldPop data set (www.worldpop.org). We extracted a road (comprising national and state highways) and railways network from the online information portal India Under Construction (Nayak et al., 2020), and validated the layers visually with satellite imagery. We then calculated the linear infrastructure density (including both roads and rail) at the same 1-km^2 pixel level across the landscape using QGIS 3.12.0 (QGIS.org, 2019). We also calculated the Euclidean distance to elephant habitat (forests and grasslands), and to human habitation or settlements.

Land-management practices and regional policies are often broad-scale, and dependent on the predominant land uses or devised and implemented based on specific land uses. The major and most conservation-relevant land uses in our landscape were croplands (predominantly rice paddy), tea plantations and closed-canopy plantations (including rubber *Hevea brasiliensis*, teak *Tectona grandis* and sal). Assessing the relative contribution of these land uses to connectivity can have significant management value. Therefore, there are benefits to comparing a model that only considers land use/land cover (LULC) as a covariate, with models that include other environmental and anthropogenic covariates; such a comparison can allow us to evaluate what improvements these additional environmental and anthropogenic covariates can provide to LULC-only data and models often used to inform management. We were, thus, interested in evaluating a logistic regression model built just using LULC variables and comparing it to models that incorporate other relevant covariates.

To do this, we further classified our study region into user-defined LULC classes, namely: (i) cropland (predominantly rice paddy), (ii) closed-canopy plantations (including rubber, teak and sal), (iii) tea plantations, (iv) forests, (v) grasslands, (vi) human habitation, (vii) water and (viii) barren land (predominantly river sand islands), at a 20-m resolution. We collected a total of 4,547 training points from field surveys and photo interpretation of satellite imagery. We used spectral bands from the remotely sensed imagery described above, as well as the derived Enhanced Vegetation Index. To improve classification, especially in regions of high cloud cover, we additionally used data from the Sentinel-1 SAR GRD C-band (Erinjery et al., 2018; Torres et al., 2012). We also derived a series of textural indices, including the Index-based Built-up Index (Xu, 2008), and the

Modified normalized difference water index (Xu, 2006), which have been shown to provide for more accurate classification of specific LULC classes (Poortinga et al., 2019). We used the Random Forest algorithm (Breiman, 2001) for classification, trained with 500 decision trees, including variables listed above, after checking for collinearity and variable importance.

We extracted the modal or most represented LULC within the same 1-km^2 square window described above. Sampled locations with modal LULCs other than closed-canopy plantations, tea plantations or croplands were removed from the analysis due to low sample size; these represented 4.6% of sampled points.

We used logistic regression to model the effect of the above-described covariates on elephant presence at sampled locations. We constructed biologically plausible models, which included individual covariates and all permutations of additive effects of the same (Table S1). We tested for collinearity amongst covariates before including them in our models. Since LULC was correlated with the calculated Enhanced Vegetation Index, we did not include these two covariates in the same model; closed-canopy plantations had higher EVI than tea plantations, followed by croplands (rice paddy fields). We assessed model support using Akaike's Information Criterion (Burnham & Anderson, 2002).

2.4 | Parameterising landscape resistance

For each 1-km^2 pixel in our landscape, we extracted values of the covariates used in our models, as described above. We then predicted the probability of elephant use of these pixels by model averaging the estimated probability of use parameter, using model weights w_i, across all models in our model set (Burnham & Anderson, 2002). We considered this probability of elephant use of a grid cell to represent its conductance; resistance was calculated as the inverse of the conductance (McRae et al., 2008). We thus obtained a model-averaged *resistance map* of our study region.

To assess resistance based solely on LULC, we considered the probability of elephant use of a pixel—as estimated by the LULC-only model based on the LULC of the pixel—as conductance. Resistance was calculated as the inverse of this value. We scaled these resistances by a factor of 10—that is, we multiplied the calculated resistances by a factor of 10—to better highlight differences on a resistance scale of 1–100. This also placed the LULC-based resistances on a scale comparable to model-averaged resistances, and thus facilitated comparison of the two scenarios. Resistances for forests and grasslands—which represent potential habitat and are known to have negligible resistance—were set to a value of 1; resistance for habitation—which is known to be actively avoided by elephants—was set to the highest resistance value as obtained from the model-averaged resistance map. Water—in our landscape, the Brahmaputra River—and barren land (sand islands in the Brahmaputra River) were considered to represent barriers to elephant movement.

2.5 | Modelling connectivity

We identified source patches as important elephant habitats distributed across the study region with known elephant populations, primarily from Forest Department records, available literature and secondary information (e.g. media reports of elephant presence or conflict). These were typically individual protected areas or multiple contiguous protected areas that spanned more than 100 km^2; we also included two smaller habitat patches in the important Kaziranga–Karbi Anglong ER, a landscape known to house a substantial elephant population (Goswami et al., 2019). In total, we identified 10 source patches, nine of which are forest habitat, and one, a forest–grassland mosaic habitat. The source patches included, from west to east: 1. Garo Hills forests; 2. Reserve Forests (RFs) in Boko-Chhaygaon Revenue Circles, Kamrup Rural District; 3. Garbhanga RF; 4–5. Kholahat RF, split into two patches due to structural discontiguity between the two patches; 6. Jungthung and surrounding RFs; 7. Bagser RF; 8. Kaziranga National Park (the forest-grassland mosaic habitat); 9. Wildlife Sanctuaries (WLS) and Reserve Forests (RFs) in the Kaziranga–Karbi Anglong ER (North Karbi Anglong WLS, Panbari RF, and parts of East Karbi Anglong WLS and Kaliyani RF); and 10. Nambor WLS (Figure 1b). Sources patches were digitised from available maps of protected areas in the region (Anon, 2019), and matched visually to satellite imagery and the classified LULC map. The Garo Hills forests fell outside the area we sampled but represented an important known source patch with dispersal linkages to sampled locations. Ignoring this habitat with known elephant presence would lead to the omission of important connectivity areas, and hence it was included as a source. Source patches were digitised using QGIS 3.12.0 (QGIS.org, 2019). The above-described source patches also represented our set of destination patches.

We used the randomised shortest path (RSP) framework to model connectivity (Kivimäki et al., 2014; Panzacchi et al., 2016). The RSP model works on a network characterised by nodes, which represent each pixel in our study region, and edges, which determine the links between pixels. Each pixel in our study region was linked with its eight neighbours. The inverse of the mean resistance of the two neighbouring pixels was assigned as the edge weight, scaled to values close to 1.

We used a series of six θ values altogether—5, 1, 10^{-1}, 10^{-5}, 10^{-8}, 10^{-12}—as we had source patches that were separated by Euclidean distances ranging from as low as half a kilometre between Kaziranga National Park and the Karbi Anglong forests, to as high as 337 km between Nambor Wildlife Sanctuary and Garo Hills. The θ value determines the trade-off between optimal (when θ values are high) and random (when θ values approach 0) movement. Intermediate θ values then would represent an arguably more realistic scenario where dispersers have some (but not complete) knowledge of the landscape; that is, dispersers make movement decisions based on partial information limited to a perceptual window around them (henceforth referred to as a scenario of "partial disperser information"; see informed dispersal: Clobert et al., 2009). The absolute value of θ that corresponds to each of these scenarios (optimal movement →

partial disperser information → random walk) would depend on the size of the modelled landscape and corresponding resistance values (Panzacchi et al., 2016), relative to the animal's ability to perceive and navigate the landscape (for example, its perceptual window and ranging capabilities). Our landscape had source population pairs, which were separated by small, as well as large distances; hence we considered θ values of 5 and 1 to be representative of optimal movement, at small and large spatial scales, respectively. Given the scale of our study region and the ecology of our study species, we considered a θ value of 10^{-1} and 10^{-5} as scenarios of partial disperser information. Finally, we considered θ values of 10^{-8} and 10^{-12} to represent random walks or near-random walks, with dispersers only having knowledge of their immediate surroundings. Similar θ values have been used elsewhere (Panzacchi et al., 2016).

We modelled animal movement between each source-destination pair, for each pixel; this value represents the expected number of *passages* across all paths between the source and destination node. We obtained a cumulative passage map, for each θ value, by summing across all source-destination pairs.

2.6 | Model comparison and validation

In addition to comparing model support for the LULC-only model with other models in our logistic regression model set via Akaike's Information Criterion, as described in Section 2.3, we made the following comparison to assess the utility of adding complexity to connectivity modelling. We compared passage values estimated from the model-averaged resistance map, with those from the LULC-only map. Since a typical management implication of connectivity modelling is the identification of corridors, or priority connectivity areas, we also compared identified corridors (defined as locations with top 10% passage values) from the model-average results, with that of the LULC-only model, across θ values. Finally, we calculated a probability of omission, or the probability that a corridor, as identified based on model-averaged resistances, will be omitted when using a model based solely on LULC.

Ideally, we would have validated model predictions with independently collected data on elephant movement. In the absence of such data, we investigated the passage value corresponding to each of our recorded elephant presence points (Peck et al., 2017). To do this, we first cropped the passage map from the RSP model for each θ value to our sampled area, defined as a minimum convex polygon around our sampled points. We excluded habitation and forest as our sampling framework excluded these areas. We converted passage values in the resultant map to percentile-passage values. We extracted mean percentile-passage values in a 1-km^2 buffer around each of our recorded presence points. We compared these percentile values, corresponding to elephant presence points in the matrix, across θ values. We did this for predictions from the model-averaged resistances, as well as from those based on LULC alone. We distinguished low-frequency sightings (<100 elephants) from high-frequency (≥100 elephants) sightings; the higher number

here typically indicated that a large number of elephants (more than can be counted or recalled) were seen, rather than the exact number of elephants sighted. This distinguishes areas occasionally used by elephants—including for movement—and those frequented by elephants, such as frequently used movement corridors and locations adjacent to primary habitat.

Analyses were carried out in R 4.0.2 (R Core Team, 2020) and RStudio 1.3 (RStudio Team, 2020), using packages raster (Hijmans, 2020), rgdal (Bivand et al., 2020), rgeos (Bivand & Rundel, 2020), rasterVis (Lamigueiro & Hijmans, 2020), gdistance (van Etten, 2017), gridExtra (Auguie, 2017), AICcmodavg (Mazerolle, 2020), and dependencies.

2.7 | Threats to connectivity

The impact of linear infrastructure on connectivity is increasingly recognised. To assess the potential for an expanding network of linear infrastructure to impede connectivity in our study region, we overlaid the road and railways network on our flow map.

Human–elephant conflict can be a potential barrier to connectivity (Ghoddousi et al., 2021; Goswami & Vasudev, 2017). We compared conflict locations, as recorded during our questionnaire survey, to percentile-passage values predicted from model-averaged resistances for all six θ values, as calculated above (in Section 2.6). We also visually represented the overlay of conflict on our flow map. Using data on reported conflict from our questionnaire surveys, we generated a heatmap based on a kernel density estimation, with a radius of 5 km; a distance of 5 km has been previously reported to be a meaningful scale for spatial patterns of human–elephant conflict (Gubbi, 2012; Guerbois et al., 2012). As conflict values were a direct representation of what we observed—rather than a prediction—we restricted our inference on conflict to the strict confines of our survey grid. For each grid cell, we extracted the mean conflict value from the heatmap described above. We overlaid this conflict heatmap on RSP-predicted passage maps.

3 | RESULTS

3.1 | Effort

In total, we interviewed 1,184 people, primarily farmers, across the sampled area of 7,150 km^2. We excluded respondents who were unable to differentiate between captive elephant detections and wild elephant detections, respondents outside Assam, and those within 1-km of neighbouring sample locations. Of the 607 respondents thus obtained, 207 (34%) reported wild elephant presence within 1 km of the respondent's location at some point of time during the past year. The median number of elephants sighted per respondent over the past year was 8. The reported number of sightings showed a bimodal distribution, with one mode at around 8 sightings in the past year, and the other at 400–500 elephants during the same

period. Our respondents were located mostly in the matrix, covering open croplands (84%), closed-canopy plantations (12%) and tea plantations (4%), and to a lesser extent, human habitation and forests (Figure 1a).

3.2 | Resistance as a function of ecological and anthropogenic covariates

There was strong support for the effect of vegetation, measured as the Enhanced Vegetation Index, human population density, and distance to forest, on elephant use of the landscape (Table 1 and S1). Models with EVI, human population density, slope and distance to forest also performed much better than a model that just considered LULC categories, demonstrating the benefit of incorporating greater information into resistance parameterisation (Table 1). Environmental and anthropogenic covariates provided more fine-scale information on resistance in our case, as compared to just using LULC categories (Figure 1b and S1).

EVI had a strong positive effect on elephant use of a spatial location such that areas with more vegetation had a higher probability of elephant use (Table 2). There was also support for a negative effect of human population density and distance to forests on elephant use of locations: elephants used areas closer to forests and with lower human population densities (Tables 1 and 2). There was some support for a negative effect of slope, wherein steeper areas tended to be less used by elephants (Table 1 and 2). Whilst the density of linear infrastructure and distance to human habitation were included in models with ΔAIC < 2, we believe these two covariates to be uninformative parameters (Arnold, 2010) and therefore expected to have little influence on movement (Fullman et al., 2017). This expectation is supported by the fact that model deviance was not substantially reduced with the addition of these covariates (Tables 1 and S1), and that the estimated coefficients for these covariates were close to 0, with 95% confidence intervals overlapping 0 (Table 2).

We estimated model-averaged conductance for each 1-km^2 grid cell in our study region using model weights (Table S1), and pixel-specific covariate values (Table S2). We calculated resistance as the inverse of conductance. The resistances thus obtained ranged from 1 to 138.41 (Figure 1b).

3.3 | Resistance as a function of LULC

We attained a classified land use/land cover (LULC) map with eight classes, with relatively high overall accuracy of 0.96 and a κ statistic of 0. 95. LULC impacted elephant presence—the difference in AIC between the intercept-only model and a model with LULC as the only covariate was 31.77 (Table 1). The LULC-only model did not however receive support when compared to the best-supported models in our model set (ΔAIC = 52.97, Table 1). As per the LULC-only model, elephants used tea plantations for movement with relatively high propensity, followed by closed-canopy plantations, and

TABLE 1 Model selection statistics for the logistic regression analysis used to assess the effect of covariates on elephant presence, including the number of parameters K, Akaike's Information Criterion (AIC), ΔAIC, AIC weights w_i, and model deviance. We show models with ΔAIC < 10, along with the LULC-only and the intercept-only model

Model	K	AIC	ΔAIC	w_i	Deviance
EVI + slope + population + dist$_{forest}$	5	693.63	0.00	0.31	683.63
EVI + slope + population + dist$_{forest}$ + dist$_{habitation}$	6	694.81	1.18	0.17	682.81
EVI + slope + population + dist$_{forest}$ + dens$_{linear}$	6	695.20	1.56	0.14	683.20
EVI + population + dist$_{forest}$	4	695.85	2.22	0.10	687.85
EVI + slope + population + dist$_{forest}$ + dist$_{habitation}$ + dens$_{linear}$	7	696.44	2.81	0.08	682.44
EVI + population + dist$_{forest}$ + dens$_{linear}$	5	696.97	3.34	0.06	686.97
EVI + population + dist$_{forest}$ + dist$_{habitation}$ + dens$_{linear}$	6	697.84	4.20	0.04	685.84
EVI + dist$_{forest}$	3	700.27	6.64	0.01	694.27
EVI + dist$_{forest}$ + dens$_{linear}$	4	700.41	6.78	0.01	692.41
LULC + slope + population + dist$_{forest}$ + dist$_{habitation}$	7	702.34	8.71	0.00	688.34
LULC + slope + population + dist$_{forest}$	6	702.81	9.18	0.00	690.81
LULC	3	746.60	52.97	0.00	740.60
Intercept-only model	1	778.37	84.74	0.00	776.37

Abbreviations: EVI, Enhanced Vegetation Index; population, human population density; dist$_{forest}$, distance to elephant habitat (forests and grasslands; dist$_{habitation}$, distance to human settlements or habitation); dens$_{linear}$, density of linear infrastructure (roads and railways); LULC, land use land cover.

lastly, open cropland (Table 2). The resistances of these three land uses were set to 14, 18 and 35, respectively (Figure S1).

3.4 | Connectivity

Passage across each of our map pixels for the different θ values, as predicted from the RSP framework based on model-averaged resistances, are shown in Figure 2. Whilst forests were used by animals more frequently for movement (Figure S2), other land uses also served to facilitate movement. This was especially true under scenarios of lower θ values (Figure 2). The same is shown for passage based on resistances predicted from LULC alone (Figure S3).

Recorded presence points overlapped higher percentile passage values, particularly for the scenario where $\theta = 0.1$, and when considering model-averaged resistances (Figures 3a and S4). This scenario had no reported NA values—NA values arise when the RSP model is unable to predict movement across all source-pairs—and a relatively high proportion of reported presence points showing high percentile passage. This indicates that models of optimal movement and partial disperser information, show more support than those of random movement. The same pattern is seen for predicted passage from the LULC-only RSP model, wherein $\theta = 0.1$ had relatively high percentile passage values and no NAs (Figure S4).

Passage values predicted by the model-averaged resistances, correlated with those predicted by LULC alone, but also showed substantive differences (Figure S5). Predicted corridors (top 10% passage values) similarly showed some overlap, but not entirely (Figure 3b). The probability of omission, that is, the probability of being identified as a corridor when using model-averages resistances but being missed by LULC-only predictions, was 0.26.

We zoom into important landscapes, showing the scenario of $\theta = 0.1$, based on model-averaged resistances (Figure 4). The first is centred around the Kaziranga–Karbi Anglong ER, arguably the most important landscape for elephants in the region (Goswami et al., 2019). The second landscape shows the forests stretching east of Reserved Forests (RFs) in Boko–Chhaygaon Revenue Circles towards Garbhanga and Kholahat RFs, including forests in the Dhansiri–Lumding ER. The third landscape includes RFs in Boko–Chhaygaon Revenue Circles stretching westwards up to Garo Hills. Modelled passage suggests that the strongest movement links are amongst forests in and around the Kaziranga–Karbi Anglong landscape, and forests of the Garo Hills are relatively isolated from other parts of our study region.

3.5 | Threats to connectivity

Whilst we did not find support for the effect of linear infrastructure density on elephant use of the landscape, roads and railways do cut across certain important connectivity areas (Figure 4).

Recorded conflict locations overlapped more with areas of high predicted percentile passage, as compared to areas of lower percentile passage, especially under scenarios of higher θ values (Figure 5a). The spatial overlap between connectivity and conflict is not straightforward. Clearly, certain landscapes—the more fragmented ones towards the west—face higher conflict, as compared to more stable landscapes such as the Kaziranga–Karbi Anglong Elephant Reserve (Figure 5b). Because we only assessed conflict within the spatial domain of our survey responses, we note that our inference on the interplay between conflict and connectivity is limited.

TABLE 2 Covariate effects on elephant presence as estimated by (a) models with ΔAIC < 2, and (b) the LULC-only model. 95% confidence intervals are indicated in parenthesis

Model	Intercept	Population	EVI	dens$_{linear}$	dist$_{habitation}$	slope	dist$_{forest}$
(a)							
EVI + slope + population + dist$_{forest}$	-1.87 (-3.15, -0.60)	-0.09 (-0.15, -0.02)	9.00 (5.13, 12.87)			-0.09 (-0.18, -0.00)	-0.43 (-0.60, -0.26)
EVI + slope + population + dist$_{forest}$ + dist$_{habitation}$	-1.97 (-3.27, -0.68)	-0.08 (-0.15, -0.01)	8.68 (4.75, 12.60)		0.03 (-0.04, 0.10)	-0.09 (-0.17, 0.00)	-0.42 (-0.59, -0.25)
EVI + slope + dens$_{linear}$ + population + dist$_{forest}$	-1.85 (-3.12, -0.58)	-0.08 (-0.15, -0.01)	8.95 (5.09, 12.81)	-0.02 (-0.07, 0.03)		-0.09 (-0.17, 0.00)	-0.43 (-0.61, -0.26)
(b)	Intercept (croplands)		Closed-canopy plantations		Tea plantations		
LULC	-0.91 (-1.10, -0.72)		1.19 (0.69, 1.69)		1.72 (0.87, 2.58)		

Abbreviations: EVI, Enhanced Vegetation Index; population, human population density; dist$_{forest}$, distance to elephant habitat (forests and grasslands); dist$_{habitation}$, distance to human settlements or habitation); dens$_{linear}$, density of linear infrastructure (roads and railways); LULC, land use land cover.

4 | DISCUSSION

Connectivity is a core component of most landscape-scale conservation programmes, especially those that are planned in the light of predicted land-use change, habitat fragmentation and climate change (Doerr et al., 2011; Keeley et al., 2019). However, connectivity conservation practice on the ground has been severely limited by our (in)ability to prioritise areas that are beneficial for connectivity from a functional standpoint (Keeley et al., 2018; Vasudev, Fletcher, et al., 2015). This is particularly true for tropical landscapes, where habitat is highly fragmented and interspersed with areas of high human density. In this context, our findings provide a feasible and valuable approach to model regional connectivity for a wide-ranging species like the Asian elephant, generating information that is directly relevant to region-wide conservation planning. Whilst forested corridors are important (e.g. Vasudev et al., 2021), there is increasing recognition of the utility of the matrix in facilitating animal movement and adding redundancy—which enhances resilience of connectivity—to animal pathways (Fletcher et al., 2014; Hilty et al., 2020; McRae et al., 2008). Our findings are particularly relevant to assessing the importance of animal movement through the non-habitat, human-modified matrix.

Connectivity modelling typically suffers from data paucity (Sawyer et al., 2011; Zeller et al., 2012), though there do exist examples of connectivity models that are well-informed by animal movement data (e.g. Fletcher et al., 2014; Panzacchi et al., 2016; Revilla & Wiegand, 2008). Sampling in the non-habitat areas, where knowledge of permeability is uncertain, is difficult, especially with respect to recording infrequent events of dispersal. Crowd-sourced data are a valuable source of information in this context, and we show that such data are amenable to connectivity modelling of detectable and charismatic species like the Asian elephant. Indeed, at the scale of large regions, and for species that have captured the interest of the general public, crowd-sourced information has provided data and scientific insights that otherwise may have been logistically difficult to obtain (Brown et al., 2018; Frigerio et al., 2018).

Our survey provides us with valuable insights into environmental and anthropogenic drivers of elephant use of locations across our region and shows that there is substantive benefit to adding such information to connectivity models. EVI emerged as a strong driver of resistance, highlighting the importance of vegetation—in forests as well as on private multiple-use or plantation lands—for landscape-scale conservation. This finding was reaffirmed by the additional role of distance to forests on elephant use of the matrix. As elephants are wide-ranging and capable of traversing large distances, this effect is likely to be a manifestation of high perceived risk in the matrix.

We used our survey data to perform a form of validation of our connectivity models and discriminate between different θ values. Ideally, we would have validated modelled passage with independent empirical data, such as elephant movement routes recorded using telemetry devices, camera trapping along potential corridors or observational follows (e.g. Panzacchi et al., 2016). Such independent validation can strengthen our results, and deviations from predicted passage may provide further insights into elephant movement behaviour; in turn,

FIGURE 2 Passage, as estimated from the randomised shortest path (RSP) model, based on model-averaged resistances estimated from our logistic regression model set, where (a) $\theta = 5$ and (b) $\theta = 1$ represent scenarios akin to optimal movement, and (c) $\theta = 10^{-1}$ and (d) $\theta = 10^{-5}$ represent scenarios of partial disperser knowledge within a perceptual window about the study region, whilst (e) $\theta = 10^{-8}$ and (f) $\theta = 10^{-12}$ represent scenarios akin to random movement
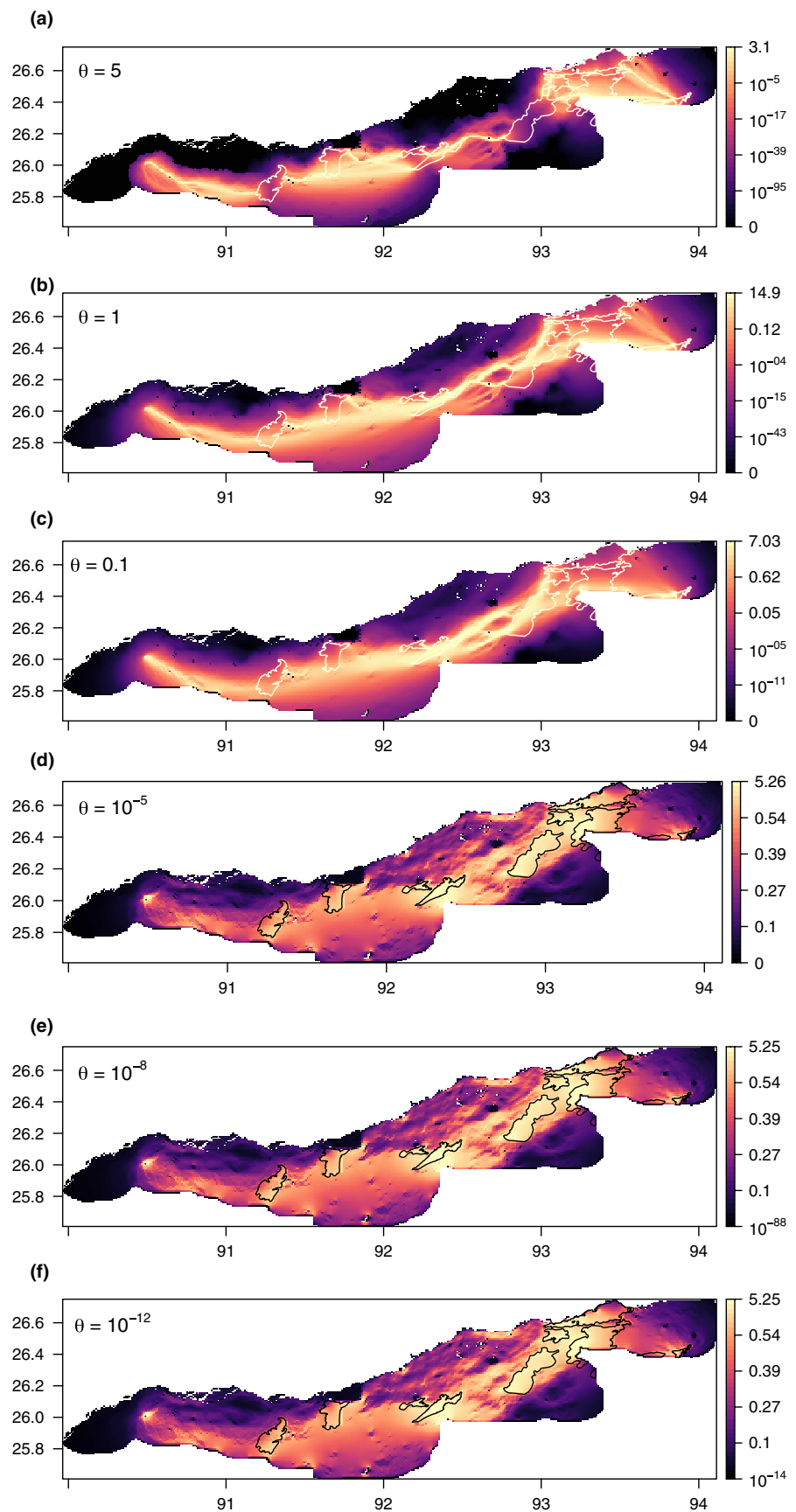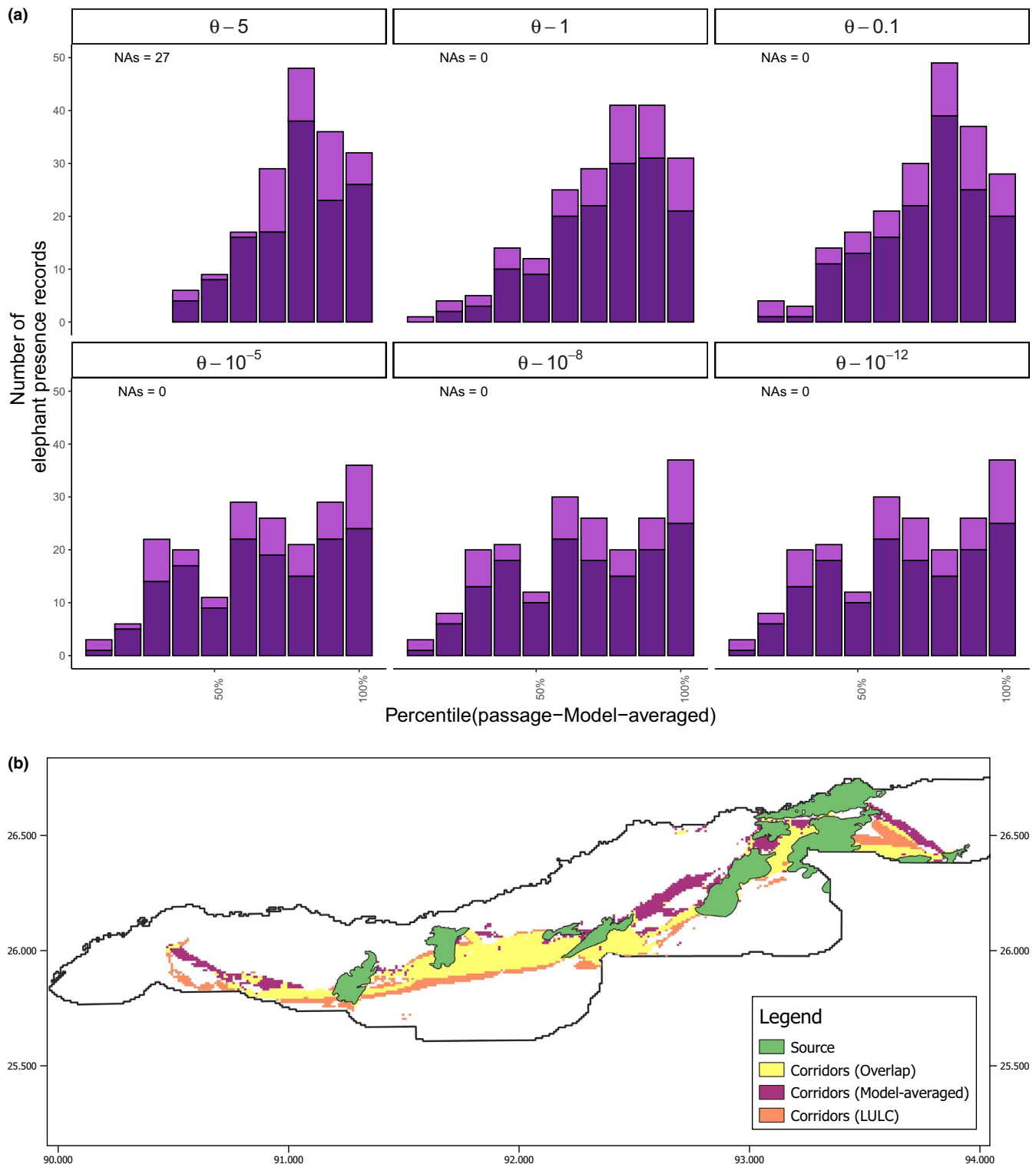
FIGURE 3 (a) Comparison of the RSP model based on model-averaged resistance values across θ values, as percentile passage values for recorded low frequency (dark purple, <100 elephants) and high frequency (light purple, ≥100 elephants) elephant presence points. (b) We show corridors (top 10% passage value) as predicted based on model-averaged resistance values, the LULC-only model, and the overlap between the two, combined across all θ values

this information can feed into a revised resistance map. Thus, we see connectivity maps as evolving with improved knowledge on elephant movement behaviour, as well as changing environments and elephant adaptation to a modified landscape.

The question of how animals move has always been one of interest to scientists (Nathan et al., 2008) as it shapes fundamental aspects of species ecology, distribution and evolution (Clobert et al., 2012; Peterson et al., 2011). In more recent times, this

FIGURE 4 Linear infrastructure, in the form of roads (shown as yellow dashed lines) and rails (shown as white dotted lines) overlaid on passage, as modelled by randomised shortest path (RSP) models, based on model-averaged resistances under a scenario that likely represents partial disperser information (i.e. $\theta = 10^{-1}$), for (a) the landscape including Kaziranga NP, WSs and RFs in Kaziranga–Karbi Anglong ER, and neighbouring forests, (b) forests stretching east of RFs in Boko–Chhaygaon Revenue Circles towards Garbhanga and Kholahat RFs, including forests in the Dhansiri–Lumding ER, (c) RFs in Boko–Chhaygaon Revenue Circles stretching westwards up to Garo Hills, and (d) the entire study region. We show extents of the three landscapes in panel (d)
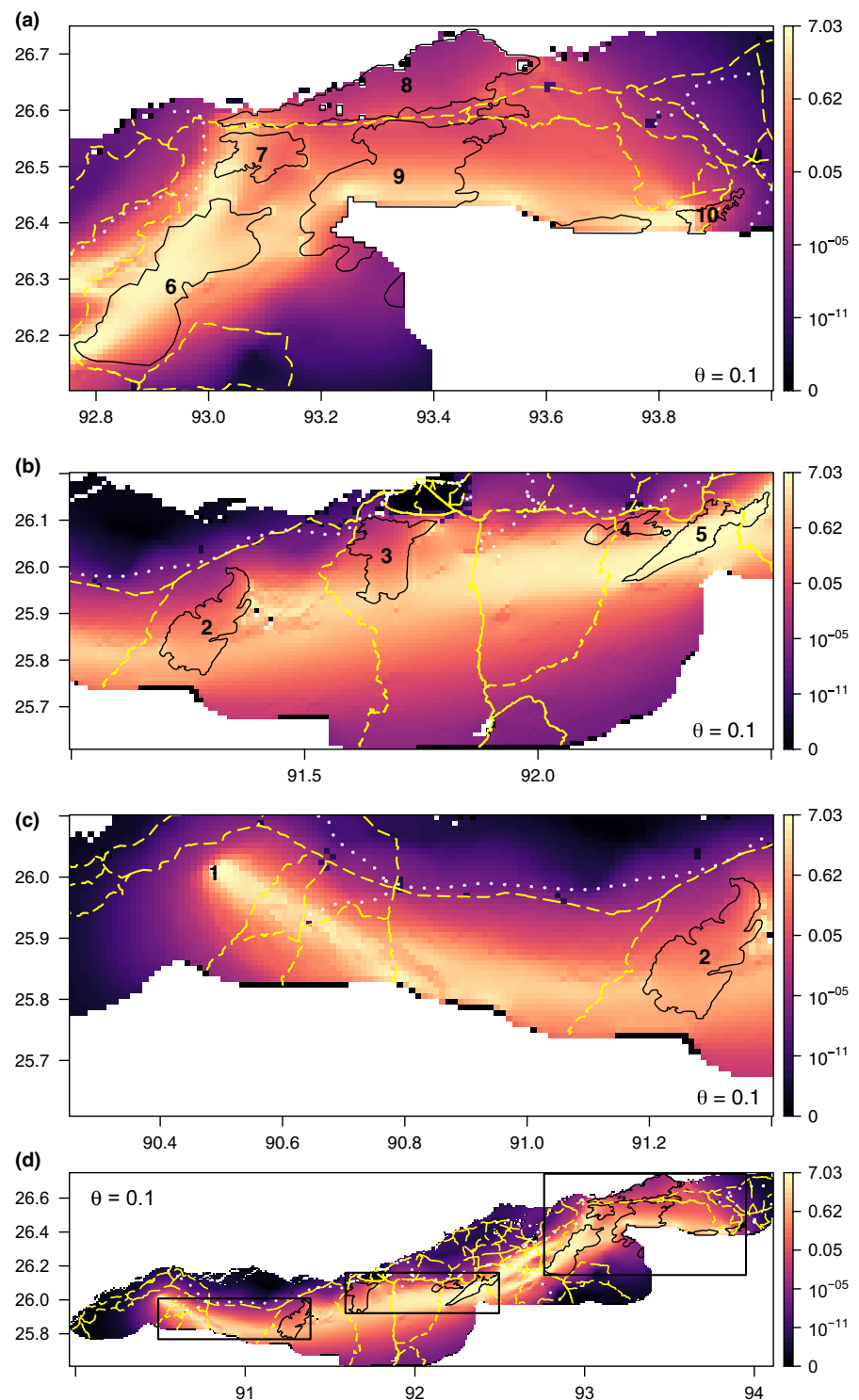
question has taken on significant conservation value. For both reasons, the past few decades have seen vast developments in animal movement models (Fletcher et al., 2019; McRae et al., 2008; Panzacchi et al., 2016). The RSP framework used here presents a useful and flexible approach to modelling animal movement, explicitly stating assumptions on animal perception of the landscape (Kivimäki et al., 2014). It is worthwhile to note here, that other animal movement models—ranging from least-cost (Adriaensen et al., 2003), resistant-kernel (Compton et al., 2007), agent-based

(Revilla & Wiegand, 2008), or circuit-based modelling (McRae et al., 2008)—all make assumptions about animal perception of the landscape. The RSP framework makes these assumptions explicit, and in so doing, can be adapted to animals and landscapes fitting various scenarios of disperser perception of their environment, via changing θ values. Choosing appropriate θs, however, remains an unresolved issue, with no clear guidelines yet on what represents ideal values. Our findings suggest that elephants move optimally, or with partial information of the landscape, rather than as random
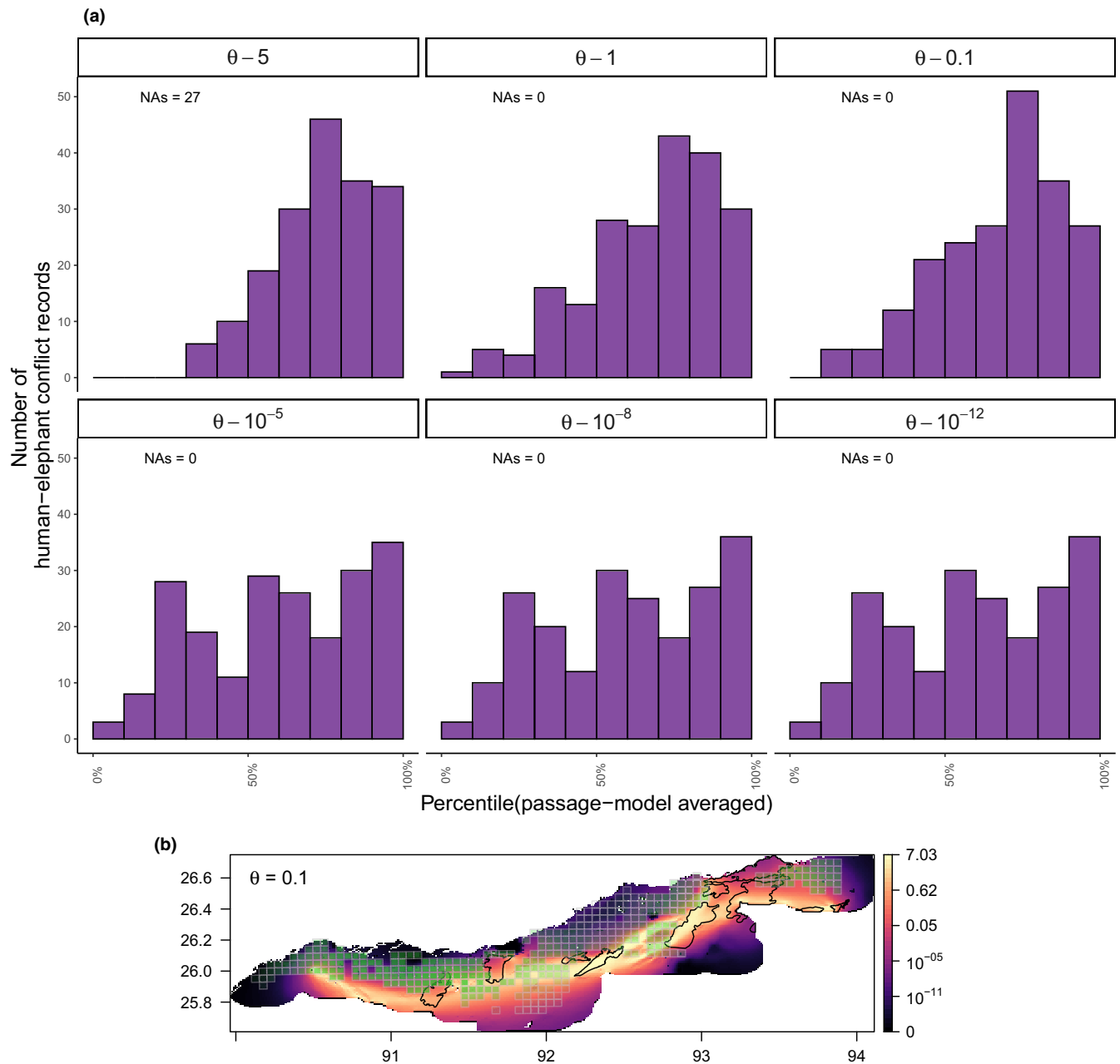
FIGURE 5 (a) Percentile passage values for recorded conflict points for each θ value, as predicted by the RSP model based on model-averaged resistances. (b) We also overlay conflict hotspots from our surveyed locations on predicted passage, from an RSP model with $\theta = 10^{-1}$ and model-averaged resistances. Conflict is determined by our questionnaire data, represented by green grid cells, wherein the less transparent the grid cell, the greater the reported conflict

walks (Figure 3a). This finding aligns with what we know about elephant biology, though much of our knowledge is gained from African elephants: elephants have high cognitive and perceptive abilities (Plotnik & de Waal, 2014), store and share substantive knowledge accumulated over a long lifespan with their herd via social cues (McComb et al., 2001), and use spatial memory to determine movement paths (Polansky et al., 2015). With further information on elephant movement decisions, and their perceptual windows, we hope to be able to fine-tune our estimation of appropriate θs.

Whilst there are differences between passage maps under different scenarios of θs, there is a utility for these maps, both to identify optimal movement routes that can help prioritise important forested corridors (Figure 2a and b), as well as more diffuse routes relating to movement with partial information (Figure 2c) for conservation interventions targeting matrix permeability. The difference between these maps shed light on the reliance of elephants on forests as corridors, highlighting their importance, whilst also recognising the conservation role of the matrix for elephant movement (Driscoll et al., 2013; Lees & Peres, 2008; Vasudev et al., 2021). Going into

the future, connectivity conservation efforts must be two-fold. One, they must secure forests that clearly forge important linkages between habitat patches. Simultaneously, efforts must be invested in the matrix to retain or even improve the permeability of these lands to movement, thus securing their role in landscape-scale conservation of endangered species.

Elephants have a complex relationship with people; whilst revered, they also are prone to enter into conflict with people (Vasudev et al., 2020). It is, thus, useful to examine the overlap between conflict and connectivity (Figure 5b), so as to tailor conflict mitigation strategies that allow elephant movement. There are clear differences across landscapes in terms of conflict incidence, with the more fragmented landscapes to the west having higher intensity of conflict. We note that our conflict data are based on direct observations and restricted to our sampled grid cells, rather than being a prediction of conflict intensity across the entire study region. We also did not explicitly account for conflict or conflict mitigation measures in our estimation of resistance. For these reasons, we are not able to emphatically state that conflict is impeding connectivity (or not) from our current models. Nonetheless, we note that conflict, and conflict mitigation measures, do have the potential to pose a barrier to connectivity (Goswami & Vasudev, 2017; Osipova et al., 2018)—elephants were found to avoid areas of high human population density in this study, corroborating earlier research that supports the same observation (Goswami, Sridhara, et al., 2014; Goswami et al., 2021). It is arguably in this context that fine-scale prioritisation is most useful in informing local-scale actions, as well as regional policy for both connectivity conservation and conflict mitigation. Such prioritisation could form the basis for participatory conservation measures on the ground that allows for animal movement and connectivity whilst minimising conflict (e.g. Vasudev, Goswami, et al., 2015).

We modelled the effect of linear infrastructure density on elephant use of the landscape, but the model including this covariate received weak support, and the covariate is likely to be an uninformative parameter. We note that impacts of linear infrastructure are probably best assessed through studies at finer scales than the one we used, and through methodological approaches that assess fine-scale movement behaviour of elephants (e.g. using telemetry) rather than based on their presence alone. At such a scale and with fine-grained information, we expect that movement may be predicted to be severely restricted by roads and rails. We overlaid linear infrastructure on modelled elephant passage and found roads and rails to intersect movement zones in the study region. We note that currently, linear infrastructure in Northeast India is relatively less developed than the rest of the country (Nayak et al., 2020) but is expected to substantially expand in the future. Linear infrastructure expansion that does not consider elephant connectivity needs is likely to impact the species by both blocking important movement routes, and by increasing dispersal mortality. Such expectations are supported by research that highlights the negative impacts of ecologically uninformed planning of linear infrastructure on wildlife (van der Ree et al., 2015).

The Anthropocene has demonstrably restricted animal movement (Tucker et al., 2018). With ongoing and widespread environmental change, fragmentation of habitat, and climate change, the importance of connectivity is only emphasised within conservation plans (Goswami et al., 2021; Keeley et al., 2019). Increased hostility in people–wildlife interactions can exacerbate the loss of connectivity, whilst evidence on the impacts of linear infrastructure on both animal movement and survival is mounting. Modelling of connectivity across large scales is clearly important and useful, not just for connectivity conservation per se, but also for habitat preservation and conflict mitigation. As we improve models of animal movement, our ability to shape holistic conservation at landscape scales, and thus achieve conservation success, is enhanced.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13419.

DATA AVAILABILITY STATEMENT

Data used in the paper are shared as Table S2. The Supplementary information includes code to conduct the analyses described in the paper (Table S3).

ORCID

Divya Vasudev 🆔 https://orcid.org/0000-0002-8430-9667
Varun R. Goswami 🆔 https://orcid.org/0000-0003-2575-7301
Biang La Nam Syiem 🆔 https://orcid.org/0000-0002-2492-5708

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BIOSKETCH

The authors are part of a research group interested in landscape-scale conservation of species, and in developing and applying sound methodologies to inform on-ground conservation action. Their work is largely based in Northeast India, a biodiversity hotspot and important conservation region. D.V. is a landscape ecologist who is particularly focussed on connectivity modelling and conservation. V.R.G. is a population ecologist who specialises in elephant ecology, behaviour and conservation in heterogeneous landscapes. B.L.N.S. is a Ph.D. Student at Deakin University, with interests in land management practices on community-owned lands with particular emphasis on birds. A.S. and N.S. are keen on studying mammal ecology and conservation in tropical landscapes. Author webpages can be found at https://www.conservationinitiatives.org/our-team.

Author Contributions: D.V. and V.R.G. conceived and designed the project; V.R.G. and A.S. undertook fieldwork; all authors analysed the data and contributed to writing the manuscript.

SUPPORTING INFORMATION

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