

Large frugivorous birds facilitate functional connectivity of fragmented landscapes

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Summary

1. Quantifying ecosystem functions in spatially explicit ways is important for management decisions in increasingly fragmented landscapes. Between-patch dispersal of seeds by frugivores constitutes a key ecosystem function to ensure connectivity for fleshy-fruited plants. However, to date, methodological hurdles have limited our understanding of dispersal pathways on the landscape scale.

2. We made use of newly available tracking devices and combined movement data of 30 trumpeter hornbills *Bycanistes bucinator* with gut passage times and high-resolution habitat data in a fragmented forest landscape in South Africa. We identified each potential seed dispersal path and distinguished whether potential seed transport happened to a different forest patch (between-patch dispersal), within the same patch (within-patch dispersal) or into the habitat matrix (failed dispersal). To quantify functional landscape connectivity, we identified all possible between-patch connections and used graph networks to estimate landscape connectivity provided by hornbills.

3. Although potential between-patch dispersal events were rare (on average 7% compared to 20% failed dispersal and 73% within-patch dispersal), hornbills could cover distances of up to 15 km. Hornbills visited over 100 forest patches and connected a habitat network with an extent of about 50 km, which increased the potential functional connectivity of the landscape more than twofold.

4. We identified habitat patches that were critical stepping stones for seed dispersal pathways. Without these stepping stones, the network would likely disintegrate into separated components and lead to isolation of forest fragments.

5. *Synthesis and applications.* We showed that large frugivorous birds can greatly improve functional connectivity for fleshy-fruited plants across broad scales, linking habitat patches in fragmented forest landscapes. Combining high-resolution movement and landscape data in graph networks allows identifying seed dispersal pathways and critical stepping stones in fragmented landscapes. This approach addresses the general challenge of spatially explicit mapping of ecosystem services and can be widely incorporated in reserve design and landscape-level conservation planning.

Key-words: ecosystem services, hornbills, landscape connectivity, landscape fragmentation, movement ecology, seed dispersal, South Africa

Introduction

Seed dispersal by frugivorous animals is critical for ecosystem functioning, especially in the tropics as most tropical and many subtropical trees depend on seed dispersal

by frugivorous animals, often birds (Howe & Smallwood 1982; Herrera 2002; Levey, Silva & Galetti 2002; Forget *et al.* 2011). Since tropical forests become increasingly fragmented into small patches (Foley *et al.* 2005; Mayaux *et al.* 2005), frugivores play an even more important role as they have the potential to facilitate seed dispersal among forest fragments (i.e. patches). Without seed dispersal, the

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isolation of forest fragments limits the exchange of propagules, which can have severe demographic and genetic consequences (e.g. Howe & Miriti 2004). In addition, gene flow among fragmented populations is important to allow trees to adapt to changing environmental conditions (Cain, Milligan & Strand 2000; Nathan 2006). The ability of species to move to new ranges in order to keep within preferred climatic conditions is especially critical considering future climate change scenarios (Loarie *et al.* 2009; Hof *et al.* 2011; Kremer *et al.* 2012; McConkey *et al.* 2012). For animal-dispersed plant species in fragmented landscapes, this is only possible by between-patch movements of frugivores (Damschen *et al.* 2008). Assessing how frequently frugivorous birds move seeds between forest fragments and identifying between-patch pathways through the landscape will thus be key for the management of tropical trees in a changing climate.

If a bird ingests tree seeds (and the seed is not destroyed upon ingestion) in a fragmented landscape, in principle, three scenarios are possible: seeds could be moved until they reach a different forest patch. This constitutes between-patch dispersal and facilitates not only gene flow and recruitment, but it also allows range adjustments in the wake of climate change. Ideally, each patch is frequently connected with many other patches via seed dispersal by frugivores to safeguard from fragment isolation and allow range adjustments. Secondly, a seed could be moved from the parent tree, but is deposited in the same patch where it originated. Within-patch dispersal allows for recruitment away from the parent tree but no long-distance movement or gene flow among patches. Finally, dispersal fails if ingested tree seeds are moved outside the patch where they originated but are deposited in the inhospitable matrix habitat.

Several studies demonstrate that large fruit-eating bird species such as hornbills in South-East Asia and Africa, and toucans in the Neotropics are able to fly between forest patches of fragmented landscapes and have the potential to act as long-distance seed dispersers (Kemp 1995; Powell & Bjork 1995; Holbrook & Smith 2000; Graham 2001; Chaves-Campos, Arevalo & Araya 2003; Price 2006; Kays *et al.* 2011; Lenz *et al.* 2011). In addition, previous studies have investigated seed dispersal patterns of trees by combining distributions of movement data of birds and gut passage times (GPTs) of seeds (Murray 1988; Kays *et al.* 2011; Lenz *et al.* 2011). This approach has been used mostly for quantifying short-distance seed dispersal within forest patches (Murray 1988; Sun *et al.* 1997; Holbrook & Smith 2000; Westcott & Graham 2000; Westcott *et al.* 2005).

However, to date, long-distance dispersal among habitat patches has been difficult to quantify and has been less studied (but see Gomez 2003; Spiegel & Nathan 2007), in particular because movement data for birds were not available in the high temporal and spatial resolution necessary to track between-patch movements. To our knowledge, no previous study has used movement

data and GPTs for quantifying the frequency of between-patch dispersal, spatially explicit mapping of seed dispersal paths among forest patches, and for quantifying the degree to which large frugivorous bird movements could increase landscape connectivity. These types of information will be critically important for management of fragmented landscapes where maintaining landscape connectivity and ecosystem services is a key for conservation activities.

We studied seed dispersal by trumpeter hornbills *Bycanistes bucinator* along the eastern coast of South Africa. Trumpeter hornbills are the largest obligate frugivorous birds in South Africa and reach high abundances in the coastal and riverine forests of KwaZulu-Natal (Kemp 1995; Bleher *et al.* 2003). The forest fragments of south-eastern South Africa are a global hot spot for tree diversity (Mittermeier *et al.* 2004), but after decades of human land use, these forests are heavily fragmented and only a few natural forest patches remain today (Eeley, Lawes & Reyers 2001). The study area is thus ideal to investigate seed dispersal in fragmented landscapes.

We tracked movement patterns of hornbills and used data from Lenz *et al.* (2011) on feeding trials of captive birds to assess GPTs. We combined distributions of movement patterns and GPTs to derive potential seed dispersal events (Lenz *et al.* 2011). We also used high-resolution habitat data to classify the landscape into forest patches (i.e. habitat that allows natural recruitment of tree seeds) vs. matrix habitat. We evaluated whether potential seed transport ended in a different forest patch (between-patch dispersal), within the same patch (within-patch dispersal) or into the habitat matrix (failed dispersal). We used these analyses to create graph networks (Calabrese & Fagan 2004) to estimate functional landscape connectivity, that is, connectivity measures that are not just based on the physical landscape features, but consider actual movement paths of organisms in the landscape.

We conducted our analyses with two goals in mind: (i) we aimed to investigate questions related to the frequency of between-patch dispersal: How frequently do between-patch dispersal events occur compared to within-patch and failed dispersal? Is landscape configuration, that is, between-patch distance, critical for dispersal events? Are there seasonal differences in the frequency of between-patch dispersal events? Overall, we expected less between-patch dispersal in the breeding season when birds are more restricted to nest sites and ranging behaviour may be significantly reduced compared to the non-breeding seasons. Plants that fruit mostly during the hornbill breeding season may be negatively affected by such seasonality. (ii) We asked questions related to the location of potential dispersal pathways through the landscape. Are there forest patches that represent critical stepping stones for landscape connectivity? Finally, we aimed to quantify the increase in landscape connectivity, comparing landscape connectivity with and without between-patch seed dispersal by hornbills.

Materials and methods

STUDY AREA AND HABITAT

The study area lies at the east coast of South Africa in KwaZulu–Natal centred on the Oribi Gorge Nature Reserve *c.* 100 km south of Durban and 20 km inland from Port Shepstone. The area features subtropical coastal scarp forest with some of the highest tree diversity on earth (Mittermeier *et al.* 2004).

Large natural forests lie in deep gorges and on steep slopes (e.g. Oribi Gorge Nature Reserve, Mbumbasi Nature Reserve). These nature reserves are surrounded by intensively farmed land, mostly sugarcane plantations. Within the agricultural matrix, there are small remnant patches and strips of natural forest. In addition, the farmhouses in the agricultural areas often have large gardens that contain both indigenous and exotic fruit-bearing trees. Climate change is expected to have severe consequences for these forests making significant altitudinal and latitudinal shifts of tree species necessary (Eeley, Lawes & Piper 1999).

To map and distinguish habitat that is suitable for natural recruitment of indigenous fruit-bearing trees from areas that are unsuitable, we used the KwaZulu–Natal land-cover data set based on SPOT satellite imagery (GeoTerraImage, Pretoria, South Africa) as a base layer. We defined as suitable habitat areas that were categorized as forest (indigenous), dense thicket and bush (70–100% canopy closure) and medium bush (<70% canopy closure; in the following all termed forest). For all other land-cover classes, successful natural establishment of a dispersed seed is very unlikely (e.g. sugarcane plantations, rural areas, farm gardens, roads), and we grouped them collectively as matrix habitat. Since the land-cover data set has a rather coarse resolution of 20 m, we acquired high-resolution Quickbird imagery (GISCOE, Gauteng, South Africa) for the entire study area (a total of 142 Quickbird scenes) with a resolution of 60 cm to refine our habitat map. This imagery allowed a much finer delineation of habitat edges. We visually inspected all locations hornbills had visited (see description on hornbill movements below) and used on-screen digitizing (i) to adjust edges of all forest patches hornbills had visited and (ii) to correct for possible habitat misclassification of the coarser base layer.

HORNBILL MOVEMENT AND GUT PASSAGE TIME

Trumpeter hornbills are the largest obligate frugivorous birds in South Africa and are among the most abundant frugivores in the study area (Kemp 1995). From 2008 to 2011, we caught trumpeter hornbills with mist nets throughout the study region, around Oribi Gorge Nature Reserve and around the coastline, during the breeding and non-breeding seasons. We equipped male birds with backpack style GPS loggers (see also Lenz *et al.* 2011; which uses a subset of the data used for analyses in this paper). We did not track females since the data logger may interfere with their breeding behaviour. GPS loggers were programmed to measure the position of birds at 15-minute intervals throughout the day. At night, when hornbills do not move, we did not record any positions. GPS relocations were downloaded remotely via VHF receivers. Median measurement error of the logger location was 8.0 m (25% quartile: 4.5 m; 75% quartile: 14.0 m, see Lenz *et al.* 2011). Since it was not necessary to recapture birds and we were able to relocate all birds and download their data, we achieved a representative sample of movement distances without

a bias in favour of short distances (as is the case with traditional ground-based telemetry methods).

Hornbills almost exclusively feed on fruits even throughout the breeding season, and their large gape width also allows them to swallow and transport large seeds (Kemp 1995). We used GPT data of feeding trials from Lenz *et al.* (2011). They determined the distribution of GPTs for trumpeter hornbills (median: 57 min; minimum: 15 min; maximum: 155 min). This distribution was derived from a mix of different fruits sizes, types and digestion modes (regurgitated vs. defecated). Since Lenz *et al.* (2011) did not find any significant difference of maximum or median GPTs among different fruit types, fruit sizes or digestion mode, we assumed that the distribution we used is generally representative for natural fruits.

FREQUENCY AND LIMITATION OF BETWEEN-PATCH DISPERSAL

To quantify the frequency of and identify limiting factors for between-patch dispersal, we calculated potential seed dispersal distributions by combining the individual displacement distributions of each bird with the GPT distribution. We used only days for which we had at least 30 relocations and eliminated the first 3 days of tracking when movement distances were shorter (see Lenz *et al.* 2011). We randomly selected a thousand starting points in the movement track of each bird. We then drew a time interval from the distribution of observed GPTs (ranging from 15 to 150 min) to identify an endpoint on the bird's movement track and calculated the Euclidean distance between each starting point and endpoint (Westcott *et al.* 2005; Spiegel & Nathan 2007; Lenz *et al.* 2011). Since seed dispersal cannot originate from the habitat matrix, starting points were only allowed when they were located in a forest patch. For each event, we then recorded whether it ended in a different patch than where it had originated, in the same patch or in the habitat matrix. This procedure weighted the distribution of movement distances with the GPT distribution and allowed us to model how often dispersal events occurred that constituted between-patch dispersal compared to within-patch dispersal and failed dispersal. We did not track seeds directly, nor did we assess the likelihood that seeds that had been moved by hornbills established themselves, thus we investigate potential functional connectivity.

We also investigated effects of landscape configuration and seasonality. We compared between-patch dispersal distances with patch-to-all-other-patches distances and patch-to-nearest-patch distances. We calculated centroid-to-centroid as well as edge-to-edge distances for all those patches that had been visited by hornbills. If distance among patches mattered and dispersal occurred mostly from one patch to the nearest neighbouring forest patch, we expected shorter distributions of successful between-patch dispersal events compared to patch-to-all-other-patches distances. Accordingly, we expected similar distributions of between-patch dispersal events compared to patch-to-nearest-patch distances. Finally, we compared seasonal differences in the frequency of between-patch dispersal. Since birds are bound to the proximity of the nesting site in the breeding season, we expected less between-patch dispersal in the breeding season than in the non-breeding season.

FUNCTIONAL CONNECTIVITY AND MAPPING DISPERSAL PATHWAYS

To calculate the degree to which hornbills raised functional connectivity in the landscape, we used all tracking data and identified

every potential seed dispersal path, that is, every movement within 150 min that ended in a different forest patch than where it had originated. We mapped all these possible connections and generated a spatially explicit, binary, non-directed graph network (Calabrese & Fagan 2004). Using node- and link-weighted network measures (Rayfield, Fortin & Fall 2011), we compared landscape connectivity with and without between-patch seed dispersal by hornbills. Specifically, we calculated the integral index of connectivity (*IIC*, eq. 1, Saura 2008; Saura & Rubio 2010; Baranyi *et al.* 2011) as:

$$IIC = \frac{\sum_{i=1}^n \sum_{j=1}^n \frac{a_i a_j}{1+n_{ij}}}{A_L^2} \quad \text{eqn 1}$$

where n is the total number of nodes (i.e. forest patches) in the landscape, a_i and a_j are the area sizes of nodes i and j , n_{ij} is the number of links in the shortest path (topological distance) between patches i and j , and A_L is the total landscape area. This index calculates the probability that two seeds randomly placed within the landscape fall into the same forest patch or forest patches that are connected via dispersal links. The index is bounded by 0 and 1, where 1 would indicate a landscape that is entirely occupied by habitat and 0 would indicate a landscape where no habitat is available. The index accounts for both topology and area size of patches as it integrates patch area and connectivity between habitat patches in a single measure and estimates possibilities for dispersals between all pairs of patches (Pascual-Hortal & Saura 2006). The *IIC* index is applicable to any landscape graph and can evaluate the importance for maintaining overall connectivity of any landscape element or combination of landscape elements (Pascual-Hortal & Saura 2006). We used the software Conefor Sensinode 2.6 (Saura 2008) to calculate *IIC*. We calculated the total landscape area used by hornbills with an alpha convex hull (disc radius: 3 km) encompassing all hornbill relocations.

We identified critical stepping stones for seed dispersal by calculating betweenness centrality for each patch, that is, the number of geodesics or shortest paths going through a patch (library 'igraph' in R, R Development Core Team 2012) and identifying those forest patches in the upper five percentile of betweenness centrality.

Results

We tracked 30 birds, 9 in the breeding and 21 in the non-breeding season with a total of 543 tracking days and 23 794 relocations. For the frequency analyses, we refined the data (see Materials and methods) and had data of 461 tracking days.

We identified 103 forest patches that were visited by hornbills. These patches constitute a few larger forest blocks within the nature reserves and many smaller fragmented patches in the habitat matrix. The mean patch size was 2.16 km² (median 0.06 km², min: 0.0016 km², max: 74.29 km²).

Overall, 7% of all potential dispersal events constituted between-patch dispersal. However, that proportion varied by season, and only 4% of all dispersal events in the breeding season were predicted to be between-patch dispersal compared to 8% in the non-breeding season

(Fig. 1). Twenty per cent of all dispersal events were predicted to end in the habitat matrix (failed dispersal). That means that about 27% of all dispersal events left a forest patch and 73% of all potential dispersal events occurred within the same forest patch. Again, that proportion varied by season with almost all potential dispersal events, that is, 93%, in the breeding season being within-patch dispersal, compared to only 67% in the non-breeding season.

Between-patch dispersal (median = 1513 m, min = 77 m, max = 14 790 m, Fig. 2) had the longest distances, compared to failed dispersal (median = 584 m, min = 7 m, max = 13 980 m, Fig. 2) or within-patch dispersal (median = 68 m, min = 0 m, max = 5103 m, Fig. 2). Likewise, patch-to-all-other-patches distances (based on patch centroids, median = 15 110 m, min = 75 m, max = 48 710 m, Fig. 3) were considerably greater than between-patch dispersal distances. However, patch-to-nearest-patch distances were slightly shorter (median = 728 m, min = 75 m, max = 5413 m, Fig. 3) than between-patch dispersal distances. Results remained qualitatively the same when edge-to-edge rather than centroid-to-centroid distances were used (see Fig. S1 in Supporting information). We consider the centroid-to-centroid rather than the edge-to-edge distances more suitable for comparisons with dispersal, because the dispersal distances indicate potential dispersal to and from any location in a patch rather than edge-to-edge distances.

All between-patch dispersal across distances > 3 km happened in the non-breeding season (non-breeding season: median = 1722 m, min = 77 m, max = 14 790 m; breeding season: median = 858 m, min = 207 m, max = 2240 m).

The graph analysis showed that out of 103 forest patches visited by hornbills, 100 patches were connected via hornbill movements within the range of GPTs (max = 150 min). We detected 233 links among forest patches that were potential seed dispersal paths (Fig. 4). Three patches were isolated with no potential seed dispersal to or from the other 100 patches. Potential seed dispersal paths ranged from Oriibi Gorge Nature Reserve

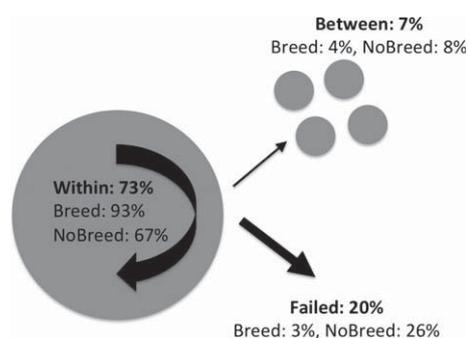


Fig. 1. Proportion of potential between-patch dispersal compared to within-patch dispersal and failed dispersal ending in the landscape matrix. Potential between-patch dispersal occurred on average to four different patches. Breed: breeding season, NoBreed: non-breeding season.

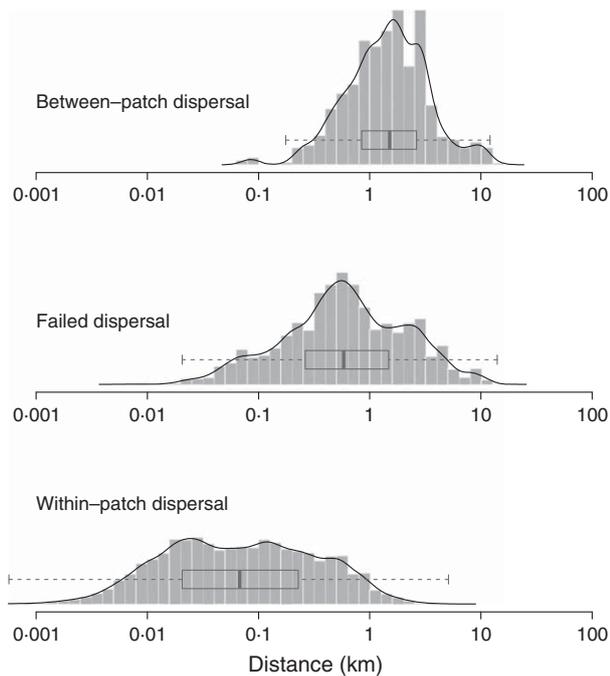


Fig. 2. Distribution of potential between-patch dispersal distances compared to failed dispersal distances (i.e. dispersal events that leave a forest patch but end in the habitat matrix) and potential within-patch dispersal distances. Boxplots indicate range, quartiles and median of distributions.

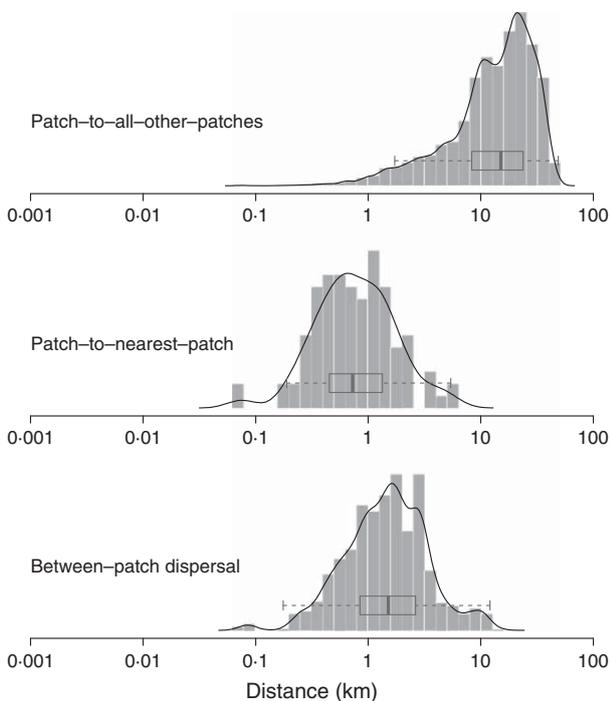


Fig. 3. Patch-to-patch distances compared to nearest-patch distances and potential between-patch dispersal distances. Boxplots indicate range, quartiles and median of distributions.

along three corridors all the way to the coast (Fig. 4). The main, central corridor included Mbumbasi Nature Reserve located in between Oribi Gorge and the coast

(Fig. 4). The habitat matrix between forest patches along these corridors consists mostly of residential areas and farmlands. For example, Mbumbasi Nature Reserve is surrounded by densely populated built-up areas providing almost no natural forest strips. Northwards of Oribi Gorge lays the forested valley of the Mzimkhulu River, which was less visited by the trumpeter hornbills. Importantly, movement happened in both directions, and hornbills that were caught at the coast (Fig. 4) moved all the way to Oribi Gorge and vice versa. Overall, dispersal movement of hornbills connected a network of forest patches that spans about 50 km in north-south and 30 km in east-west direction (compared to capture locations that spanned 29 and 11 km respectively, Fig. 4).

On average, each patch was connected to 4.5 other patches via dispersal links. However, the standard deviation was high with 5.2 dispersal links. Fifteen out of the 103 patches had connections to only one patch or were fully isolated. Likewise, the betweenness centrality varied widely among patches with a median of 1 and a maximum of 3304. The overall network diameter, that is, the longest topological distance from one end to the other of the network, was nine links.

We identified six forest patches in the upper five percentile of betweenness centrality that were stepping stones having a great number of geodesics (shortest paths) from all nodes (i.e. forest patches) to all others that pass through that node (Fig. 4). The two nature reserves in the area, Oribi Gorge and Mbumbasi Nature Reserve, were two of these critical stepping stones facilitating dispersal in all directions. Additionally, we identified four smaller patches as stepping stones (Fig. 4), one in the direct neighbourhood of Oribi Gorge and three located close to the coast. The three patches at the coast were critical for connectivity towards the larger patches of forest in the southern part of the study area (Fig. 4).

The forest area of the 103 visited forest patches covered 73% of the entire landscape area measured as an alpha convex hull around all hornbill relocations. The connectivity of the landscape measured as *IIC* without hornbill dispersal was 0.099. If the links among patches of the sample of between-patch dispersal events of hornbills were included (Fig. 4), that probability increased more than twofold to 0.24. If we removed the links provided through the six stepping-stone patches identified above, the network fell apart and connectivity declined to 0.10.

Discussion

We showed that 30 hornbills tracked over 543 days provided potential functional connectivity to link a network of 100 forest patches ranging 50 km from north to south and 30 km from east to west. Although potential between-patch seed dispersal was relatively rare, it occurred across distances sufficiently large to connect almost all patches visited by hornbills in this highly fragmented landscape. Overall landscape connectivity measured as *IIC* increased

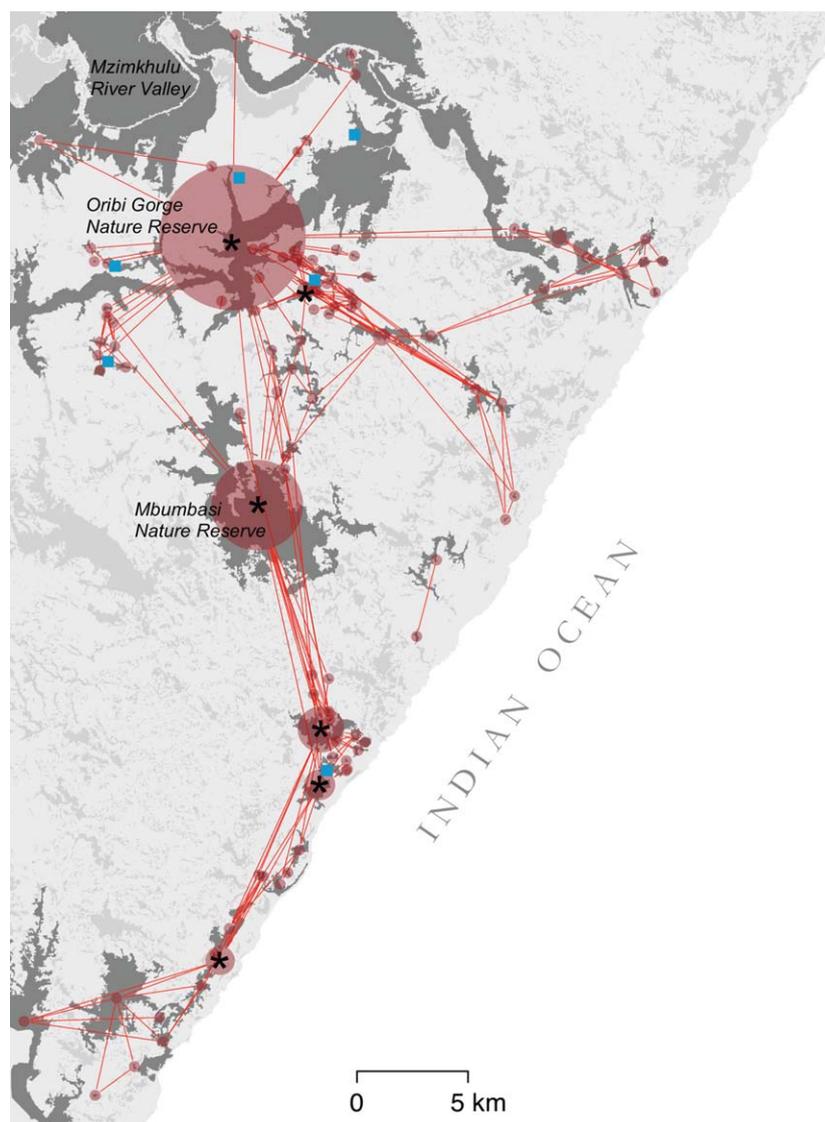


Fig. 4. Map of the study area on the east coast of South Africa in KwaZulu–Natal and seed dispersal by hornbills. Forest patches (grey) and graph network of potential seed dispersal pathways (red). Dark grey: patches visited by the tracked hornbills, light grey: other forest patches, blue: capture locations of hornbills, *: stepping stones for seed dispersal, that is, patches in the upper 5% of betweenness centrality. Red lines: potential seed dispersal paths. Red dots: nodes of network, scaled by betweenness centrality, that is, number of geodesics (shortest paths) from all nodes to all others that pass through that node.

from about 0.10 to about 0.24, and we identified critical stepping stones that were instrumental for network integrity.

The size of the network connected via between-patch dispersal and the maximum between-patch dispersal distance of about 15 km were comparable to scales of predicted climate-change-induced spatial shifts in broad leaf tropical and subtropical forests (3.3 km per decade, Loarie *et al.* 2009). This means that hornbills – under current levels of fragmentation – could potentially provide the broad-scale movements trees will need to adjust to expected shifts in their preferred climatic conditions. It is important to consider though that the network diameter was nine links: if a tree species were to travel through the entire network, it would require several iterations of seedling establishment, regrowth, fruiting and new seed dispersal. Tree species, that generally have a long generation time, would thus need centuries to travel from one end of the network to the farthest topological other end. Furthermore, to date, there is generally little evidence for

latitudinal range shifts in trees: a recent comprehensive review estimated rapid latitudinal species' range shifts of 16.9 km per decade (Chen *et al.* 2011), but did not include any plant species in this estimate. Zhu, Woodall and Clark (2012) found a general lack of response of trees to climate change across eastern North America, which may be due to the low establishment success of newly colonizing tree species compared to established species (Ibáñez, Clark & Dietze 2009).

Coastal scarp forests in KwaZulu–Natal are not only predicted to be affected by climate change, but will likely face even greater levels of fragmentation in the future (Eeley, Lawes & Piper 1999; Eeley, Lawes & Reyers 2001). Under the current levels of fragmentation, of all visited forest patches, only three were not connected to the main network. The other 100 patches had at least one connection to the network that connected all these patches with each other. However, many forest patches in the study area were not visited by hornbills at all (Fig. 4). This may be because we did not track all hornbills in the

area, because we tracked birds only for a limited time, or it may be that some of the unvisited forest patches did not constitute adequate habitat. Disentangling selection of forest patches was beyond the scope of this study, but it is important to note that it is a possibility that some of the forest patches in the study area may never be visited by hornbills. We also found that patch-to-nearest-patch distances were slightly shorter than potential between-patch dispersal distances, which suggests that potential dispersal events were not always limited to the nearest neighbour but that between-patch dispersal to other than the nearest neighbour was also likely. This was confirmed by the graph analysis, which showed that, on average, 4.5 potential connections to other neighbouring patches existed. Importantly, the maximum predicted between-patch dispersal distance (14 790 m) was greater than the greatest nearest-neighbour distance of patches (5413 m), which means that, hornbill movements could, in theory, connect all patches in the landscape with each other. That being said, in our large sample of 23 794 relocations, we did not find all patches being connected since three patches had no potential connection to the main network. Overall, our study finds that movements of hornbills are at scales sufficient to provide connectivity in this highly fragmented landscape.

Nevertheless, we also found evidence that fragmentation at present-day levels already has significant effects on the dispersal ability of hornbills: Failed dispersal had smaller distances than successful between-patch dispersal indicating that many seeds may have been deposited before a bird was reaching suitable forest habitat and that large stretches of matrix habitat may impose problems for successful between-patch dispersal. Likewise, the average patch-to-all-other-patches distances were significantly greater than between-patch dispersal distances which demonstrates that seeds would need to move through the landscape from patch to patch rather than being able to cross the entire study area within a single move.

We also point out that rates of between-patch dispersal were substantially lower in the breeding season (November–December, 4% vs. 8%, see Fig. 1) and that all between-patch dispersal across distances > 3 km happened in the non-breeding season. That implies that in the hornbill breeding season, landscape connectivity for fruiting trees may be greatly reduced and seed dispersal among patches may be extremely rare for tree species that produce fruit exclusively in the breeding season.

Another critical issue for network connectivity are stepping stones: we identified all patches in the upper five percentile of betweenness centrality (Fig. 4). These patches were instrumental for network integrity since without them the network would likely disintegrate into separated components. Two of those stepping stones were the large nature reserves in the area, Oribi Gorge and Mbumbasi Nature Reserves. These reserves were critical for providing dispersal links to neighbouring patches in their surrounding and linking them to the overall network,

which demonstrates that the importance of these reserves for plant populations goes well beyond their borders and extends to the entire region. Three other stepping stones were small forest patches at the coast. They were linking the two reserves and their neighbouring patches to larger stretches of forest in the south. Based on our movement data, that connection would have been lost without these rather small patches, and the network would disintegrate into separate components. While the importance of the large nature reserves for conservation may be apparent independent of this study, these smaller patches at the coastline have been revealed by our tracking data to be key components for plant dispersal in the study area. Protecting and maintaining these small forest patches will be important for future conservation of hornbills and plant diversity in the area.

The approach used here of combining remote sensing with animal movement and dispersal data in graph networks has implications that go far beyond the study system. A key challenge for making natural resource and management decisions more effective is the quantification of ecosystem services in a spatially explicit manner (Nelson *et al.* 2009). We here demonstrate a practical and efficient way for spatially explicit mapping of ecosystem functions that could be directly implemented in reserve design and landscape-level conservation planning. The graph approach used here demonstrates in a straightforward manner, unlike other spatially explicit studies on seed dispersal (e.g. Tewksbury *et al.* 2002; Carlo *et al.* 2013), what the loss of any particular habitat patch in a given management area would mean not just for animal movement but importantly for the functions these movements provide to maintain connectivity and biodiversity of plants. Our approach is especially applicable to other settings as the data types used for these analyses – high-resolution animal tracking as well as landscape data – become ever more abundant in research and management communities.

While combining high-resolution movement and landscape data does offer new opportunities in understanding seed dispersal, it is also important to consider the assumptions that have to be made. Generally, (i) there always will be a limited number of birds tracked over a limited time. In addition, (ii) our study considers only seed dispersal by hornbills, and (iii) investigates potential connectivity only. That means on the one hand that if more birds had been tracked or if other frugivorous bird species had been considered, the network of connected patches may increase in size and connectedness. However, the number of tracked hornbills (30 individuals) and tracking days (543) is to our knowledge by far the highest ever reported in the literature for frugivorous birds and should constitute a significant portion of hornbills in the area. In addition, trumpeter hornbills are the largest obligate frugivorous birds in South Africa, and large birds have on average larger home ranges than smaller birds (Jetz *et al.* 2004). Thus, our data shed light rather on the maximum scale at which frugivorous bird species may facilitate

functional connectivity of landscapes. Focusing on potential functional connectivity does not consider whether seeds were actually moved nor on their establishment and colonization success. For our study, we assumed that every relocation of a bird in a forest patch had the same probability of being a starting point for seed dispersal; that seeds get deposited throughout the flight; and that establishment was equally likely for all forest patches. There is evidence from other regions and hornbill species that some of these assumptions may not always be met (reviewed in Kitamura 2011). For example, in India, seeds deposited at hornbill nest sites had a higher predation rate than at the parent fruiting tree (Velho, Datta & Isvaran 2009). Nevertheless, it will be extremely difficult to obtain data on establishment success of all of the fleshy-fruited trees of the total of about 600 tree species located in this hot spot of biodiversity (Mittermeier *et al.* 2004), and it is unlikely that considering establishment success will change the overall spatial patterns in seed dispersal paths and connectivity in the landscape. To date, studies that have attempted to estimate actual vs. potential connectivity and to link dispersal mechanisms with reproduction success (e.g. Rico, Boehmer & Wagner 2012), have not used spatially explicit models for dispersal – and thus do not touch on one of the key aspects of functional connectivity covered in this study.

We demonstrate that linking high-resolution movement data and GPTs with high-resolution landscape data provides new insights into landscape connectivity. Novel bird tracking data provide unbiased estimates of long-distance movements that not only reveal how often potential between-patch dispersal occurs but also where in the landscape connections among forest patches exist. The identification of stepping stones in fragmented landscapes via spatially explicit mapping of dispersal pathways constitutes a new quality of information on landscape connectivity that will be important for future conservation management.

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Supporting Information

Fig. S1. Patch-to-patch distances compared to nearest-patch distances and potential between-patch dispersal distances based on edge-to-edge calculations.