

Evaluating realized seed dispersal across fragmented tropical landscapes: a two-fold approach using parentage analysis and the neighbourhood model

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Summary

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- Despite the importance of seed dispersal for survival of plant species in fragmented landscapes, data on seed dispersal at landscape scales remain sparse. Effective seed dispersal among fragments determines recolonization and plant species persistence in such landscapes. We present the first large-scale (216-km²) direct estimates of realized seed dispersal of a high-value timber tree (*Dysoxylum malabaricum*) across an agro-forest landscape in the Western Ghats, India.
- Based upon an exhaustive inventory of adult trees and a sample of 488 seedlings all genotyped at 10 microsatellite loci, we estimated realized seed dispersal using parentage analysis and the neighbourhood model.
- Our estimates found that most realized seed dispersal was within 200 m, which is insufficient to effectively bridge the distances between forest patches.
- We conclude that using mobility of putative animal dispersers can be misleading when estimating tropical tree species vulnerability to habitat fragmentation. This raises serious concerns about the potential of many tropical trees to recolonize isolated forest patches where high-value tree species have already been removed.

Introduction

Seed dispersal by vertebrates is the dominant mode of dispersal in dry and wet tropical forest, often with >75% of the tree species producing fleshy fruit (Howe & Smallwood, 1982; Willson *et al.*, 1989; Ganesh & Davidar, 2001). Birds are thought to be especially critical dispersal agents for maintaining tree species composition in tropical forests (Sekercioglu, 2006), but are often highly threatened by hunting or habitat degradation (Cramer *et al.*, 2007). Changes in animal abundance and movement as a result of large-scale land conversion might fundamentally alter or disrupt seed dispersal (Uriarte *et al.*, 2011; McConkey *et al.*, 2012; McConkey & O’Farrill, 2016). This can have negative consequences for recruitment of tree species (Cordeiro & Howe, 2001) and modify the forest species composition (Moran *et al.*, 2009), which underpin overall biodiversity in such landscapes. Tree species, which have highly mobile large dispersal agents, are predicted to be less sensitive to habitat fragmentation (Montoya *et al.*, 2008). However, large dispersers are often the first to be extirpated in degraded and fragmented forests (Cramer *et al.*,

2007; Kurten, 2013). In particular, such shifts from large dispersers to smaller dispersers directly reduce dispersal distances (Moran *et al.*, 2009; Markl *et al.*, 2012).

Plant species depend on seed dispersal for recruitment, recolonization and range expansion (Jordano *et al.*, 2011). Without effective seed dispersal, tree species in fragmented landscapes might be lost with considerable implications for biodiversity conservation (McConkey *et al.*, 2012). It is thus imperative to assess seed dispersal patterns if one wants to understand the implications of habitat fragmentation, to predict the probability of forest recovery on abandoned agricultural land and to implement efficient ecological restoration strategies for degraded tropical forest landscapes (Kettle, 2012). *Dysoxylum malabaricum* Bedd. ex C.DC. (Meliaceae) is a particularly interesting species in this regard as it is not only of conservation concern and economic value but is dispersed by large birds (Ganesh & Davidar, 2001). In disturbed forest it has been shown that *D. malabaricum* is predominantly dispersed by the Malabar grey hornbill (*Ocyrceros griseus* Latham) (Manjunath, 2003; Shivanna *et al.*, 2003). This hornbill species is known as a relatively strong flier crossing over varied matrices

between forest fragments, and so it is predicted to be relatively robust to land use change (Raman & Mudappa, 2003).

Seed dispersal before seedling establishment has been estimated in numerous animal-dispersed plant species by applying a wide range of observational approaches, based on disperser mobility and gut passage time, and experimental approaches using seed traps (Nathan *et al.*, 2003; Bullock *et al.*, 2006). These can often be misleading or fail to capture the relatively rare but ecologically and evolutionarily important long-distance dispersal events (Nathan *et al.*, 2003). Indirect molecular approaches using maternally inherited markers provide greater insights into historic seed dispersal (Ennos, 1994; Petit *et al.*, 2005), but often lack the resolution to investigate contemporary dispersal (but see Kamm *et al.*, 2009). Direct methods matching adult tree genotypes with fruit or seed coat tissue of maternal origin have greatly advanced our understanding of seed dispersal in temperate forest systems (Godoy & Jordano, 2001; Grivet *et al.*, 2005). However, the short-lived nature of the seeds and especially the maternally inherited seed coat in many tropical trees often makes such an approach impractical (but see Jones *et al.*, 2005 and Karubian *et al.*, 2010). Studies that apply direct estimates of seed dispersal based entirely on parentage analysis in monoecious species typically assume that the nearer candidate parent is the mother plant, inferring dispersal based upon this distance, which can again lead to underestimates of seed dispersal (Hamrick & Trapnell, 2011). Because only seed dispersal after germination and seedling establishment contributes to functional genetic connectivity, it is essential to evaluate seed dispersal at the seedling stage (hereafter called realized seed dispersal). Estimating realized seed dispersal in highly fragmented landscapes, where most of the area is unsuitable for seedling establishment, leads inevitably to a spatially clumped sampling and also to a lack of candidate parents at intermediate distances, which makes it difficult to estimate accurately the tail of the seed dispersal kernels. For all these reasons, estimates of realized seed dispersal of monoecious species in fragmented landscapes, based on genotyping of bi-parentally inherited loci, are rare (but see Aldrich & Hamrick, 1998; Bacles *et al.*, 2006; Karubian *et al.*, 2010; Sebbenn *et al.*, 2011). It is noteworthy that these previous studies cover an area more than two orders of magnitude smaller than the study presented here.

The overarching aim of this study was to evaluate how effectively seed can disperse across a fragmented agro-forest landscape. In our study system, two opposing scenarios of dispersal are conceivable. First, highly effective long-distance dispersal is expected to be carried out by larger animals with larger home ranges and higher travel velocity as well as longer seed retention (Nathan *et al.*, 2008). Several molecular studies have demonstrated this in tree species (e.g. Hardesty *et al.*, 2006; Jordano *et al.*, 2007; Kamm *et al.*, 2009). Based on observational studies, seed dispersal by hornbills is frequently found to be extensive and efficient (e.g. Whitney *et al.*, 1998; Holbrook *et al.*, 2002; Kitamura, 2011). The Malabar grey hornbill is the most important disperser of *D. malabaricum* (Manjunath, 2003; Shivanna *et al.*, 2003), is relatively large (45–50 cm and < 400 g; Kinnaird & O'Brien, 2007), is known to be a strong flier that crosses open areas (Ganesh & Davidar, 2001) and has been recorded in the study

area to occur in coffee (*Coffea canephora*) plantations as well as in sacred grove forests (Bhagwat *et al.*, 2005; Rao, 2011). Therefore, we expected that seed dispersal between the investigated forest fragments would be extensive. Alternatively, seed dispersal might be restricted because the area suitable for seedling establishment is extremely limited in the study area and fruit resources are clustered in forest fragments which might alter disperser movement. Furthermore, the start of the fruiting season of *D. malabaricum* coincides with the fledging of the Malabar grey hornbill (Murali, 1997; Mudappa, 2000) when small family flocks can be regularly observed foraging on *D. malabaricum* (pers. obs. 2009 and 2010). Such family flocks may favour areas with high fruit abundance and dense vegetation cover and therefore could have much narrower foraging ranges than single adult birds, resulting in shorter seed dispersal distances.

To evaluate these two alternative scenarios, we estimated realized seed dispersal distances in *D. malabaricum* in a complex agro-forest landscape in Karnataka, south India. Using a full inventory of all the adult trees found in 35 small forest patches over a landscape scale of 216 km², together with an extensive data set of 488 genotyped seedlings, we directly estimated seed dispersal using parentage analysis to determine the most likely parents. The genotypes of the adults and seedlings presented were previously used to explore genetic diversity parameters, fine-scale spatial genetic structure (FSGS), an indirect estimate of overall gene dispersal and the fraction of pollen dispersal between groves (Ismail *et al.*, 2012). Here, we re-analysed these previously published data to present detailed direct estimates of realized seed dispersal range and the seed dispersal kernel. In cases where one candidate parent was far from the seedling, we excluded this parent as a seed source because it violated our assumption of independent pollen and seed dispersal. To further validate the parentage-based estimates of dispersal, we additionally assessed realized seed dispersal based on the neighbourhood model implemented in the software NM+ (Chybicki & Burczyk, 2010).

Materials and Methods

Study area and study species

This study was conducted in the Kodagu district of the Western Ghats, which contains a high degree of forest cover of 46% (Garcia *et al.*, 2010). We focused on an area of intensively used landscape mosaic dominated by shade coffee plantations and paddy (Fig. 1). The study area harbours a high density of small forest patches within a complex agricultural mosaic. Within our study area, most of these forest fragments are so-called 'sacred grove' forests. These 'sacred groves' are small forest patches that have been managed and conserved by local communities for worshipping (Chandrakanth *et al.*, 2004) and are recognized as important repositories of biodiversity within an agricultural matrix (Bhagwat *et al.*, 2005).

The study area covers 216 km² where we inventorized all 235 adult *Dysoxylum malabaricum* Bedd. ex C.DC. trees; no tree was found in privately owned forest patches and only 12 were found within coffee plantations (Ismail *et al.*, 2012). This highlights the

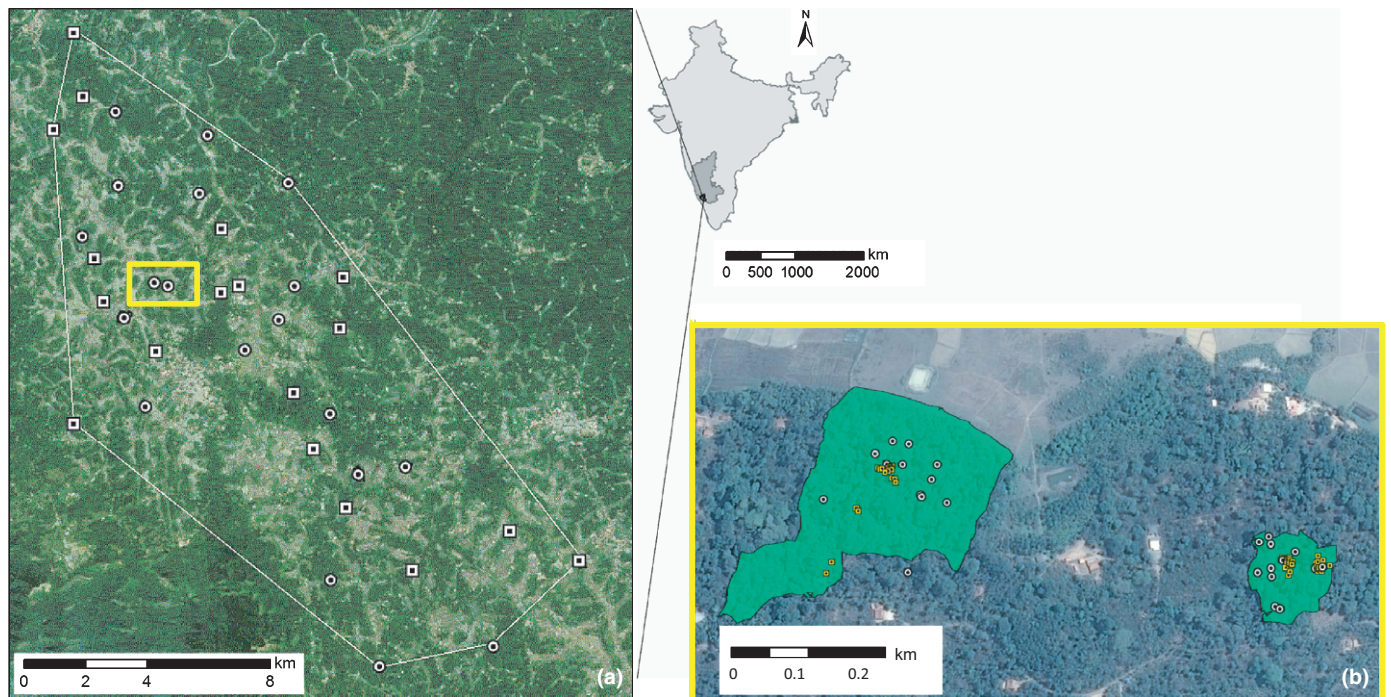


Fig. 1 Location of the study area, sample sites and seedling sampling locations. (a) The forest patches where adult trees were found within the study area delineated by a grey line (216 km²). The rectangles indicate forest patches where adult trees were sampled and the dots indicate forest patches where adult trees and seedlings were sampled. (b) A magnified image of the yellow rectangle in (a): bright green polygons indicate forest patches, dots indicate adult trees and small yellow rectangles indicate sampled seedling locations.

importance of the sacred groves as habitat for this species. The distances between the 35 forest patches which contained adult *D. malabaricum* trees ranged from 0.4 km up to 24.5 km (mean = 8.8 km; median = 7.6 km). It is noteworthy that, during this extensive systematic search for adults and seedlings, no seedlings were found in patches without adult trees. This valuable timber species is classified as endangered on the Red List published by the International Union for Conservation of Nature (Ved *et al.*, 2015). *Dysoxylum malabaricum* produces dull greenish yellow hermaphrodite flowers. The fragrance and the nectar reward suggest insect pollination, but the main pollinators are unknown. A previous study on pollen-mediated gene flow in the same study area demonstrated that *D. malabaricum* can attract pollinators over long distances, with 22% of pollen flow between groves (Ismail *et al.*, 2012). The fruit contains four carpels with two ovules each. Normally only one ovule per carpel develops into a viable seed. When ripe, the fruit splits along the septa into four sections, displaying the dark brown seeds (*c.* 30 × 20 mm) in bright orange pith (see Supporting Information Fig. S1 for an image of a ripe fruit). Two studies investigating bird visitations on *D. malabaricum* in disturbed forest recorded 65% (*n* = 206) and 93% (*n* = 149) visitation by the Malabar grey hornbill (*Ocyeroces griseus*), respectively, while most remaining visitors (32% (*n* = 100) and 6% (*n* = 10), respectively) were pigeon species which in both studies were reported to handle the fruit but not to ingest the seed (Manjunath, 2003; Shivanna *et al.*, 2003). This is in line with our own observations during seed collection in two fruiting seasons over a period of 5 wk in a total of 66 and 27 trees in 2009 and 2010, respectively. This included careful

phenological observations and searching for ripe fruit by four researchers each using binoculars and in 2010 additionally installing climbing ropes. Almost daily we observed Malabar grey hornbill family flocks during this time, while no other potential dispersers were observed. Because bird observations were made opportunistically, we cannot completely exclude occasional dispersal by other less conspicuous large bird species. However, we take these observations as a strong indication that in this study system seed dispersal is almost exclusively effected by the Malabar grey hornbill. Other less frequent but potential dispersers recorded from the study area are the mountain imperial pigeon (*Ducula badia*), green imperial pigeon (*Ducula aenea*), pompadour green pigeon (*Treron pompadora*) and the Nilgiri wood pigeon (*Columba elphinstoni*) (Bhagwat *et al.*, 2005; Rao, 2011). In less disturbed habitats, the Malabar pied hornbill (*Anthracoceros cornatus*) and the great pied hornbill (*Buceros bicornis*) might contribute to the dispersal of *D. malabaricum*, but these two hornbill species have not been recorded in the agricultural matrix or in sacred groves of the study area (Bhagwat *et al.*, 2005; Rao, 2011) and are probably absent in the study area. The Malabar grey hornbill consumes the entire seed for its brown lipid-rich seed coat which is removed before the seed is regurgitated (Manjunath, 2003; Shivanna *et al.*, 2003). Although not systematically assessed here, regurgitation times of *c.* 10 min have been reported (Manjunath, 2003). Planting trials in sterile sand of regurgitated seed versus seeds with the seed coat on reported between 92% (*n* = 44) and 100% (*N* = 20) germination success of regurgitated seed and 10% (*n* = 5 and *n* = 2) germination success of seed with the seed coat still on (Manjunath, 2003; Shivanna *et al.*, 2003).

Seeds that fall directly to the forest floor with their seed coat still on rot quickly as a result of fungal infection (Ismail, pers. obs. 2009 and 2010; Shivanna *et al.*, 2003). The strong negative effect the seed coat has on experimental seed germination in combination with the rotting of such seeds in the field suggests that efficient recruitment depends on obligate zoochory. Furthermore, secondary dispersal by rodents seems unlikely because the regurgitated recalcitrant kernels are bare cotyledons (see Fig. S2 for an image of a seed with the seed coat and after regurgitation).

Estimating realized seed dispersal

Sampling design and genotyping To collect seedling samples, we established 68 20 m × 20 m plots across 19 selected forest patches in 2009. With this sampling design, we endeavoured to represent the entire range of forest patch areas and number of adults found across our study landscape. The number of reproductive adults per patch ranged from one to 30 adults and the area ranged from 0.63 to 14.39 ha. Because seedling densities are much higher beneath fruiting trees and to ensure a sufficient number of seedlings, it was necessary to place 23 of the sampling plots directly beneath fruiting trees. The remaining 45 plots were located randomly across the selected forest patches, with at least one randomly positioned plot in each patch. These random plots ensured that we also captured seedlings dispersed further away from fruiting trees. In each plot, we collected leaf tissue from up to 20 seedlings < 50 cm in height. This sampling resulted in 313 seedlings collected beneath fruiting trees and 175 seedlings sampled in random plots. We assume that these seedlings generally represent seedlings from the two previous fruiting seasons (2007 and 2008). All 488 seedlings were mapped with a Garmin 60CSx handheld GPS (Garmin, Olathe, KS, USA) to an accuracy of 5 m.

DNA was extracted from the silica gel-dried tissue samples using a cetyltrimethylammonium bromide extraction method (Sambrook *et al.*, 1989) in the conservation genetic laboratories of the Ashoka Trust for Research in Ecology and the Environment (ATREE), Bangalore. All seedlings were genotyped at 11 nuclear microsatellite markers using the primers Dysmal 01, Dysmal 02, Dysmal 03, Dysmal 07, Dysmal 09, Dysmal 13, Dysmal 14, Dysmal 17, Dysmal 18, Dysmal 22 and Dysmal 26 (Molecular Ecology Resources Primer Development *et al.*, 2010). Details of PCR conditions are specified in Ismail *et al.* (2012).

Parentage analysis To investigate seed dispersal, we reanalysed the previously published parentage analysis of seedling samples (Ismail *et al.*, 2012) conducted with CERVUS 3.0.3 (Marshall *et al.*, 1998). The exclusion probability is 0.996 for the first parent and 0.999 for parent pairs (Ismail *et al.*, 2012). In the previous publication, this analysis was solely used to compare frequencies of inter-grove pollen dispersal at the seed and seedling stages. For each assignment, the Euclidean distance between the two most likely parents was measured; this unambiguously reveals the realized pollen dispersal distance. To ensure a high confidence in assignments, we only included the seedlings if they were assigned to two parents at the 95% confidence level.

Logical decision-based maternal tree assignment Because it is impossible to distinguish between mother and father trees with certainty based upon the offspring genotype alone, we adopted the following logical decision rules to infer the maternal tree and estimate seed dispersal distance. When both the assigned parents were found within the same forest patch as the seedling or in a different patch from the seedling, we calculated the minimum and maximum seed dispersal distances based upon (a) the mother being the nearest parent to the seedling (minimum distance) and (b) the mother being the most distant parent from the seedling (maximum distance) following Finger *et al.* (2011).

When a seedling was assigned to one parent in the same forest patch and to another parent in a different patch, we inferred that the nearest tree to the seedling was the maternal tree. This decision was based upon the assumption that pollen and seed dispersal distances are independent. To test this assumption, we conducted two linear regressions of the distances between the two assigned parents (pollen dispersal) against the two alternative seed dispersal distances (i.e. (a) the distance between the seedling and the nearer parent and (b) the distance between the seedling and the more distant parent). When we observed a strong correlation between pollen and putative seed dispersal distance, we rejected this as a realistic explanation for the maternal (seed) and paternal (pollen) relationship. That means we rejected the inconceivable pattern that hornbills systematically disperse seed from the maternal tree directly to the pollen source when one candidate parent is in a different forest patch from the seedling.

The resulting overall minimum and maximum seed dispersal distances were binned in 10-m intervals to obtain a frequency distribution on which an exponential power dispersal kernel (Austerlitz *et al.*, 2004) was fitted with the nonlinear least square method implemented in the R package NLS2 (Grothendieck, 2013). The exponential power kernel was chosen to allow comparison with the parameter estimates derived from the neighbourhood model implemented in NM+ 1.1 (Chybicki & Burczyk, 2010). Furthermore, we calculated for each patch with putative mother trees the mean minimum and maximum seed dispersal distances. We then tested in R (R Development Core Team, 2014) for significant Pearson product moment correlations of these mean minimum and maximum seed dispersal distances with patch size, number of adults and adult tree density.

Neighbourhood model To account for the lack of seedlings outside of the sacred groves and to test whether the unassigned seedlings of the parentage analysis introduced a significant bias, we computed the spatially explicit neighbourhood model implemented in the NM+ 1.1 software to estimate the parameters of the seed dispersal kernel (Chybicki & Burczyk, 2010). This model simultaneously estimates selfing rate (s), pollen migration rate (m_p), seed migration rate (m_s), average pollen dispersal distance (d_p), average seed dispersal distance (d_s), shape and scale parameters (b_p and a_p) of pollen dispersal kernels and shape and scale parameters (b_s and a_s) of seed dispersal kernels (exponential, power, Weibull, geometric or $2Dt$). The estimates of the pollen and seed dispersal kernels were based on the genotypes and

geographical locations of all the 235 adults and the 488 seedlings. Before estimating the actual parameters of the dispersal kernels, we estimated the genotyping errors with NM+ (setting the initial genotyping error rate at 0.01). Because the model is sensitive to initial values of the dispersal kernel parameters, we approximated in a stepwise approach appropriate starting values by estimating the parameter in separate runs keeping all the other parameters fixed (see Methods S1 for details of the setting of the initial starting values). Using the exponential-power function, we first estimated s , then simultaneously m_p and m_s , followed by d_p and d_s and in a last round b_p and b_s . The resulting approximated parameters of the dispersal kernels were the final starting values for simulating all six parameters simultaneously (excluding the selfing rate). This preliminary approximation was necessary to obtain starting values which allow the software to converge. This procedure was repeated with different neighbourhood sizes and the three remaining dispersal functions (Weibull, geometric and 2 D).

Data accessibility

Sample locations and microsatellite data: Dryad doi: 10.5061/dryad.3ck30.

Results

Direct estimates of pollen and seed dispersal

Of the 488 genotyped seedlings sampled across our entire study landscape, we successfully assigned the two most likely parents to 321 (66%) seedlings and one parent to 79 (16%) seedlings with high confidence (95% confidence interval (CI)). The average pollen dispersal distance (distance between the two candidate parents) was 759 m (median = 84 m). Eighty-three per cent of the seedlings assigned to two parents ($n=267$) had both candidate parents within the same forest patch as the seedling, reflecting within-patch seed dispersal. The distances between the seedling and either parent ranged from 2 to 407 m. The most conservative estimate—assuming the most distant parent was the mother (maximal distance)—gave an average seed dispersal distance of 96 m (see Fig. 2a).

In the 54 cases where one or both candidate parents were outside the forest patch of seedling collection, the regression of the distances between the two most likely parents and the distances of the seedlings to the more distant parent showed an unexpected and extremely strong linear correlation ($P < 0.0001$; adjusted $R^2 = 0.992$), whereas the alternative that the nearer parent was the seed source showed no significant correlation ($P = 0.19$;

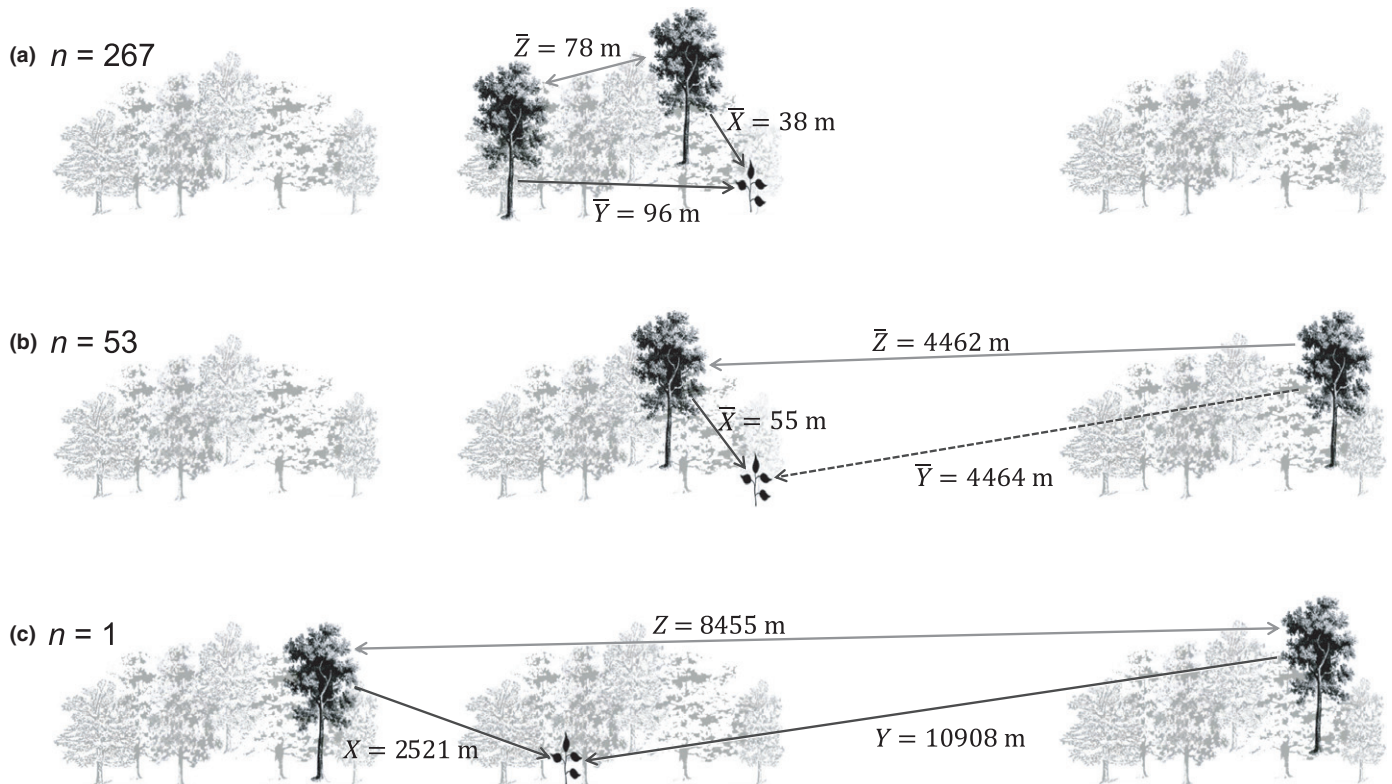


Fig. 2 Schematic illustration of minimum (\bar{X}) and maximum (\bar{Y}) mean seed dispersal estimates of *Dysoxylum malabaricum* based on the candidate parent location relative to the seedling, where: (a) both parents are in same patch (X range = 2–327 m; Y range = 7–407 m); (b) one parent is in another patch (X range = 1–194 m; in this case Y is not considered a plausible seed dispersal distance) and (c) both parents are in different patches. \bar{Z} denotes the mean distance between parent candidates, which is analogous to the pollen dispersal distance.

Table 1 Summary of the minimum and maximum realized seed dispersal distance estimates and the realized pollen dispersal estimates of *Dysoxylum malabaricum* based on parentage analysis

Candidate parent location relative to seedling forest patch	<i>n</i>	%	Minimum seed dispersal estimate (m)		Maximum seed dispersal estimate (m)		Pollen dispersal estimate (m)	
			Mean (median)	Range	Mean (median)	Range	Mean (median)	Range
Both parents in same patch	267	83	38 (16)	2–327	96 (78)	7–407	78 (66)	0–309
One parent in another patch	53	17	55 (34)	1–194	55 (34)	1–194	4462 (3645)	422–17 836
Both parents in another patch	0	0	na	na	na	na	na	na
Both parents in two different patches	1	0.3	2 521	na	10 908	na	8455	na
Total assigned parents	321	100	48 (18)	1–2521	97 (76)	1–10 908	84 (828)	0–17 836

na, not applicable.

adjusted $R^2 = 0.012$) (Fig. S3). Of these 54 assigned seedlings, 53 (17%) had one candidate parent in a different forest patch from the seedling, which could theoretically represent inter-patch seed dispersal (Fig. 2b). For these 53 seedlings, we rejected the possibility that the further parent was the seed source because this violates the assumption of independence between pollen and seed dispersal distances. Therefore, we assumed the most conservative parental relationship here, that the further parent was the paternal tree. The resulting seed dispersal distance ranged from 1 to 194 m with an average of 55 m (see Fig. 2b). Only one seedling had the two assigned parents located in different forest patches, demonstrating with high confidence inter-patch seed dispersal. In this case, the distance from the seedling to the nearest candidate parent was 2.5 km and to the furthest 10.9 km. For this seedling, we could not unambiguously discriminate between the maternal and paternal trees and therefore included in our overall estimates the nearer distance in the minimum estimate and the further distance in the maximum estimate (see Fig. 2c). Overall, the 321 assigned seedlings had a minimum average dispersal estimate of 48 m and a maximum average dispersal estimate of 97 m (see Table 1 and Fig. 3 for a summary).

Based on the parentage analysis, the scale (a) and shape parameter (b) of the exponential power kernel fitted to the maximum seed dispersal estimates were $a = 0.023$ and $b = 0.295$. For the minimum estimate, the model does not converge unless a lower bound for the scale parameter is defined. If a lower bound is defined the scale parameter drops to this bound, which we stepwise lowered to $a = 1 \times 10^{-6}$. The shape parameter for the minimum estimate was $b = 0.147$ (Fig. S4). For the pollen dispersal kernel, the scale parameter of the exponential power function was estimated as 0.009 and the shape parameter as 0.264 (Fig. S5).

Minimum and maximum estimates of realized seed dispersal distance were positively correlated with patch size ($R = 0.58$, $P = 0.012$ and $R = 0.71$, $P = 0.001$, respectively). Number of trees and density of trees showed no significant correlation with realized seed dispersal distances.

Neighbourhood model

The estimates of the pollen and the seed dispersal kernels showed the highest log-likelihood for the exponential-power

dispersal function. Neighbourhood sizes of 10 000 m resulted in the highest log-likelihoods while larger neighbourhood sizes did not converge. The estimated genotyping error rates ranged from 0% to 9.1% with an average of 3% (Table S1). The model indicates that the estimated seed dispersal kernel with a shape parameter of 0.13 (SE = 0.04) is fat tailed. The scale parameter became smaller during the approximation and dropped in the final estimate below the display threshold of 0.0001. For plotting the kernel, we applied 1×10^{-5} and 1×10^{-6} as shape parameters (Fig. S2). The seed migration rate was estimated to be 0.015 (SE = 0.007). The within-neighbourhood seed dispersal distance was estimated to be 54 m with an overall seed dispersal average of 1525 m (SE = 1567 m). The shape parameter of the pollen dispersal kernel was estimated to be 0.37 (SE = 0.04) and the scale parameter to be 10.3 (Fig. S3). The pollen migration rate was estimated as 0.16 (SE = 0.02). The estimated mean within-neighbourhood pollen dispersal distance was 258 m with an overall average of 1445 m (SE = 289 m). Interestingly, the estimate of the seed dispersal migration rate was, at 0.015 (SE = 0.007), an order of magnitude lower than the pollen migration rate (0.165; SE = 0.02). Because of the relatively high genotyping error at locus Dymal02 and locus Dymal13, we repeated the neighbourhood model without these two loci, which did not change the results qualitatively (data not shown).

Discussion

Our results support the idea that seed dispersal in *D. malabaricum* across a large landscape area appears to be very limited. This is in contrast to the scenario of efficient dispersal by a disturbance-tolerant mobile disperser. Based on parentage analysis, the majority (99.7%) of seed dispersal is within forest patches. Only in one case (0.3%) was seed dispersal between forest patches detected with high confidence, where both parents were found in a different forest patch from the seedling. Comparison of these results with seed dispersal estimates from the neighbourhood model demonstrates that seed dispersal of *D. malabaricum* in this landscape is very restricted. Below we discuss the evidence for limited seed dispersal, the more general

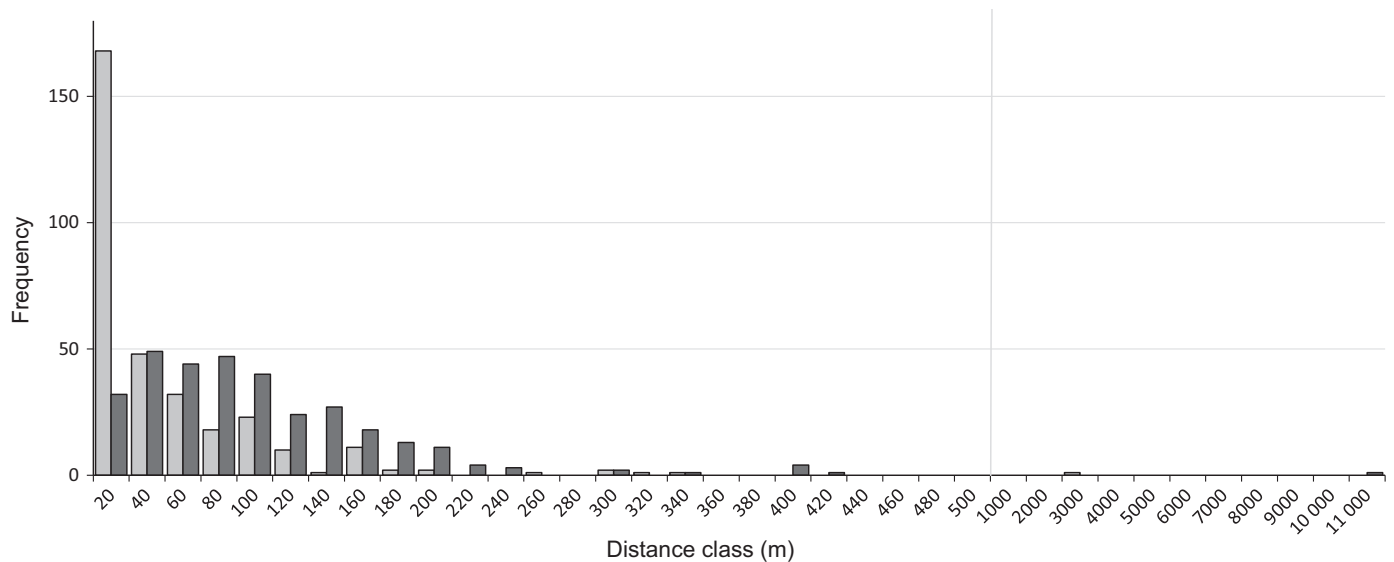


Fig. 3 Frequency of seed dispersal distances in *Dysoxylum malabaricum* ($n = 321$). Light grey bars, the minimum seed dispersal distance; dark grey bars, the maximum seed dispersal distance. Note the interval change on the x-axis after 500 m.

implications for patterns of dispersal by large birds in fragmented landscapes, and the significance of our findings for tropical forest recovery and restoration in agro-forest landscapes.

The overall estimates of maximum seed dispersal in *D. malabaricum* predict that 95% ($n = 305$) of seeds are dispersed < 200 m. When both parent trees are in the same forest patch as the seedling, at least in some cases the nearest tree is likely to be the maternal tree. Thus, our maximum estimate (Fig. 2a \bar{Y}) is probably an overestimate of mean realized seed dispersal even though it is very limited. For the seedlings where one parent was in a different forest patch from the seedling, the distinction of maternal and paternal trees greatly reduces the overall maximum mean seed dispersal estimate from 850 to 97 m. The simple test of independence between pollen and seed dispersal distances when one parent is far from the seedling is likely to significantly narrow the ranges of seed dispersal estimates in future studies of seed dispersal, especially in sparsely distributed forest species and in heavily fragmented landscapes.

The average pollen dispersal distance of 759 m (median 84 m) estimated in the seedlings is lower than previously reported values based on seed arrays (average 1.33 km; median 97 m) (Ismail *et al.*, 2012). Because the rare extreme long-distance pollen dispersal events disproportionately influence these averages, this difference does not indicate a selection against offspring derived from long-distance pollen dispersal.

The average within-neighbourhood seed dispersal distance of 54 m computed with NM+ (Chybicki & Burczyk, 2010) is within the minimum and maximum estimates we derived from the parentage analysis. The low migration rates (mean = 0.015; SE = 0.007) support the view that inter-patch seed dispersal is very rare. It is important to note that, in our highly fragmented setting, the sampling was restricted to the forest patches, resulting in a highly clumped sampling relative to the scale of the entire study area. This is illustrated by the fact that the forest patches containing *D. malabaricum* cover only 0.04% of the whole study

area. This might lead to lower precision in the estimates of the tails of the dispersal kernels, as indicated by the larger overall average seed dispersal (1524 m) and high standard error (1565 m).

Comparing the seed dispersal kernels of the neighbourhood model and the estimates based on the parentage analysis, both approaches required considerable effort to find suitable starting values to allow model convergence. This is probably also a consequence of the clumped occurrence of seedlings. It is surprising that the kernel estimated with NM+ showed even more restricted seed dispersal than when based on the parentage analysis. Despite these differences, the two independent estimates of seed dispersal provide strong evidence of extremely rare seed migration between forest patches in this landscape mosaic.

The longer seed dispersal distances in larger forest patches indicate that some longer distance primary seed dispersal into the surrounding shade coffee plantations, where seedling establishment is suppressed by regular weeding, is possible. Additionally, the positive correlation of seed dispersal distance with patch size could also be driven by predominant feeding and regurgitating of seeds within forest patches. With our data we cannot determine the relative importance of these two potential underlying processes. However, both processes are consistent with the idea that dispersal of seeds across this landscape allowing successful establishment of seedlings in suitable habitat, where adult trees are absent, is very rare.

We were able to assign a high proportion of the seedlings in our study to both parents with high confidence. The 34% ($n = 167$) of unassigned seedlings may have had one or both parents outside the study area, or one or both parents could have been logged after seedling establishment, or there could have been some genotyping error which meant they had incompatible genotypes. It seems unlikely that these 167 seedlings systematically represent long-distance seed dispersal events for two reasons. First, when simulating parentage in CERVUS 3.0.3 (Marshall

et al., 1998) with a genotyping error of 3% and with 95% of candidate parents sampled, the expected assignment rate of parent pairs is only 68%. Therefore, the 34% ($n = 167$) of seedlings not assigned to two parents is very close to the expected rate of unassigned seedlings, independent of potential cryptic seed dispersal from outside the study area. Second, if the unassigned seedlings systematically represent seed dispersal events from outside the study area, we would expect a less pronounced FSGS of the seedlings than observed (Ismail *et al.*, 2012). The unambiguous estimates of frequent long-distance pollen dispersal in the study area at the seed stage (Ismail *et al.*, 2012) and the seedling stage indicate that the pronounced FSGS in the seedlings is predominantly driven by very limited seed dispersal. Although we cannot unambiguously determine seed dispersal in the unassigned seedlings and the seedlings assigned to only one parent, there is no reason to believe that the general patterns will be different from those of the assigned seedlings. In addition, our model-based approach using NM^+ , which is not influenced by unsampled true parents, gave consistent results. In particular, the extremely low seed migration rate supports the interpretation of no significant bias from the unassigned seedlings. Interestingly, restricted seed dispersal was suggested as a likely driver of pronounced FSGS in *D. malabaricum* seedlings in four isolated populations in more continuous but disturbed forest (Bodare *et al.*, 2016). This indicates that localized seed dispersal in *D. malabaricum* is probably not a local phenomenon.

We acknowledge that the higher number of seedlings collected below fruiting trees might introduce a bias towards nondispersed seed. If the different types of plots introduce a strong bias, we would expect different dispersal distances or assignment rates. Except for the minimum estimate of the mean seed dispersal distance, we found no meaningful differences. Mean seed dispersal distances ranged from 35 m (SE = 12.5 m) to 125 m (SE = 53.5 m) in the centred plots and 69 m (SE = 6.0 m) to 117 m (SE = 7.8 m) in the random plots. The assignment rates were 65% ($n = 203$) in the centred plots and 67% ($n = 118$) in the random plots.

In comparison to previous studies on seed dispersal by hornbills (e.g. Whitney *et al.*, 1998; Holbrook *et al.*, 2002; Kitamura, 2011) our results suggest that realized seed dispersal by hornbills can be far shorter than predicted based upon observations alone. In particular, these observational studies focused on the breeding season, when male hornbills forage for long distances to feed the female at the cavity nest. It is noteworthy that seed retention times vary among tree species (Holbrook & Smith, 2000) and that the foraging range of hornbills can change dramatically over the year (Poonswad & Tsuji, 1994; Datta & Rawat, 2003). Additionally, the short regurgitation times of *c.* 10 min reported for *D. malabaricum* seed by the Malabar grey hornbill (Manjunath, 2003) indicate that when they move between forest patches they drop seeds before arriving. In the case of *D. malabaricum*, the fruiting season starts just after the fledging of the juvenile Malabar grey hornbills (Murali, 1997; Mudappa, 2000), which might restrict their foraging to the more dense vegetation of the sacred groves. Similar patterns have been shown for temperate bird species which prefer areas with high fruit abundance and

dense vegetation cover when foraging with their fledglings (Vitz & Rodewald, 2007). Because we lack a direct comparison with seed dispersal estimates from continuous forest, we cannot conclusively distinguish the relative effect of restricted initial seed dispersal shaped by hornbill behaviour from how the shortage of germination safe sites restricts realized seed dispersal in this fragmented landscape.

Localized seed dispersal has been demonstrated in temperate tree species where seeds are cached (Grivet *et al.*, 2005) and in tropical tree species based upon seed trap methods (Wenny, 2000; Cordeiro & Howe, 2001). Our study is the first large-scale study to demonstrate that in highly fragmented landscapes realized seed dispersal can be very localized, even if the size and the movement capability of the major disperser would allow otherwise. Several traits of the Malabar grey hornbill could help explain the local seed dispersal. For example, their inconspicuous plumage, a monogamous breeding system and a predominantly fruit diet (Mudappa, 2000) are associated with lower predation pressure and no need to diversify diet or to move to display perches for courtship (Pratt & Stiles, 1983). Furthermore, when fruit resources become spatially clustered, frugivores tend to forage over shorter distances (Carlo & Morales, 2008).

The minimum distance between any *D. malabaricum* tree in our study area and an adjacent forest patch is 370 m, further than 98% of our maximum estimated seed dispersal distances. Successful migration of *D. malabaricum* into forest patches where the species is not present is thus likely to be extremely rare. The absence of seedlings in forest patches where *D. malabaricum* has been logged is in line with our finding of extremely rare inter-patch seed dispersal. This lack of recolonization might be further hindered by reduced forest patch attractiveness in the absence of fruiting *D. malabaricum* trees. Considering the longevity of trees, such rare events might contribute to the persistence of the *D. malabaricum* population, but may be insufficient to maintain resilient populations and their ecosystem services.

Management intervention to ensure colonization of forest patches will be necessary to maintain connectivity and the persistence of this species (Ismail *et al.*, 2012). Human-mediated seed dispersal among forest patches by seeding or planting seedlings should be considered as one management strategy for conservation of *D. malabaricum*, especially in forest patches where there are only a few trees left.

The limited seed dispersal observed in our study not only has significant implications for recolonization and species persistence in the landscape, but may also intensify FSGS with potentially increased bi-parental inbreeding. Indeed, increased inbreeding in forest patches with only a few adult *D. malabaricum* trees causes reduced seedling performance, which potentially constrains recruitment in this species (Ismail *et al.*, 2014). Disruption of seed dispersal in fragmented landscapes has been identified as a major constraint for maintaining the adaptive potential of tree species to climate change (Christmas *et al.*, 2015). Restoration efforts such as transferring seeds among forest patches may be essential to mitigate these processes and ensure the persistence of diverse forest tree communities vital to supporting forest biodiversity in these landscapes.

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Author contributions

S.A.I., J.G., G.R., R.U.S. and C.J.K. conceived and designed the study. S.A.I. performed the fieldwork and the laboratory work and analysed the data. J.G., G.R., R.U.S. and C.G.K. contributed reagents, materials and laboratory facilities. S.A.I. and C.J.K. wrote the paper and received feedback from all co-authors.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Ripe fruit of *D. malabaricum*.

Fig. S2 Seed with seed coat and regurgitated seed without seed coat of *D. malabaricum*.

Fig. S3 Plot of pollen dispersal distance against two scenarios of seed dispersal represented by the distance of the seedling to the further candidate parent and the nearer candidate parent for the 54 *D. malabaricum* seedlings that did not have both candidate parents within the same grove based on parentage analysis.

Fig. S4 Comparison of different exponential-power seed dispersal kernels in *D. malabaricum*.

Fig. S5 Comparison of different estimates of exponential-power pollen dispersal kernels.

Table S1 Genotyping error rates estimated with NM+

Methods S1 Setting of the initial starting values for running the neighbourhood model with NM+.

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