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Testing the benefits of conservation set-asides for improved habitat connectivity in tropical agricultural landscapes

Sarah A. Scriven[1*], Kimberly M. Carlson[2], Jenny A. Hodgson[3], Colin J. McClean[4], Robert Heilmayr[5], Jennifer M. Lucey[6] and Jane K. Hill[1]

[1] Department of Biology, University of York, York, YO10 5DD, UK

[2] Department of Natural Resources and Environmental Management, University of Hawai'i Mānoa, Honolulu, HI 96822, USA

[3] Institute of Integrative Biology, University of Liverpool, Liverpool, L69 7ZB, UK

[4] Department of Environment and Geography, University of York, York, YO10 5DD, UK

[5] Environmental Studies Program and Bren School of Environmental Science & Management, University of California Santa Barbara, CA 93106, USA

[6] Department of Zoology, University of Oxford, Oxford, OX1 3SZ, UK

*Corresponding author:

Email: sarah.scriven@york.ac.uk; sarah_scriven@hotmail.co.uk;
Phone: +44 (0)1904 328632

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Abstract

1. Habitat connectivity is important for tropical biodiversity conservation. Expansion of commodity crops, such as oil palm, fragments natural habitat areas, and strategies are needed to improve habitat connectivity in agricultural landscapes. The Roundtable on Sustainable Palm Oil (RSPO) voluntary certification system requires that growers identify and conserve forest patches identified as High Conservation Value Areas (HCVAs) before oil palm plantations can be certified as sustainable. We assessed the potential benefits of these conservation set-asides for forest connectivity.

2. We mapped HCVAs and quantified their forest cover in 2015. To assess their contribution to forest connectivity, we modelled range expansion of forest-dependent populations with five dispersal abilities spanning those representative of poor dispersers (e.g., flightless insects) to more mobile species (e.g., large birds or bats) across 70 plantation landscapes in Borneo.

3. Because only 21% of HCVA area was forested in 2015, these conservation set-asides currently provide few connectivity benefits. Compared to a scenario where HCVAs contain no forest (i.e., a no-RSPO scenario), current HCVAs improved connectivity by ~3% across all dispersal abilities. However, if HCVAs were fully reforested, then overall landscape connectivity could improve by ~16%. Reforestation of HCVAs had the greatest benefit for poor to intermediate dispersers (0.5-3 km per generation), generating landscapes that were up to 2.7 times better connected than landscapes without HCVAs. By contrast, connectivity benefits of HCVAs were low for highly mobile populations under current and reforestation scenarios, because range expansion of these populations was generally successful regardless of the amount of forest cover.

4. *Synthesis and applications*. The RSPO requires that HCVAs be set aside to conserve biodiversity, but HCVAs currently provide few connectivity benefits because they contain relatively little forest. However, reforested HCVAs have the potential to improve landscape

connectivity for some forest species (e.g., winged insects), and we recommend active management by plantation companies to improve forest quality of degraded HCVAs (e.g., by enrichment planting). Future revisions to the RSPO's Principles and Criteria (P&C) should also ensure that large (i.e., with a core area >2 km^2) HCVAs are reconnected to continuous tracts of forest to maximise their connectivity benefits.

1. Introduction

Agricultural expansion has reduced the extent of natural habitats globally, and more than 12% of the Earth's ice-free land surface is now under crop production (Ramankutty, Evan, Monfreda, & Foley, 2008). With demand for cropland expected to increase (Laurance, Sayer, & Cassman, 2014), decisions about how to conserve biodiversity within agricultural landscapes are of critical importance. Conservation of biodiversity in fragmented landscapes requires that habitat networks connect remaining areas of natural habitat to facilitate range shifts under climate change (Saura, Bodin, & Fortin, 2014) and maintain meta-population dynamics (Hanski, 1994). Thus, there is an urgent need to determine how existing habitat networks facilitate movement of species across patchy landscapes (Hodgson et al., 2011).

Loss of habitat connectivity is of great concern in the tropics, where rapid expansion of commodity agriculture has resulted in widespread loss and fragmentation of forest (Hosonuma et al., 2012). In many areas, formerly extensive and contiguous forests now persist as isolated remnants scattered across vast agricultural matrices (Hill et al., 2011), and this conversion of forest to agriculture is accompanied by biodiversity losses (Laurance et al., 2014). Agricultural lands may also impede the dispersal of forest-dependent species (Scriven, Beale, Benedick, & Hill, 2017), and hence their ability to track climate change. Land-use and land-cover changes are likely to interact with climate change to exacerbate the effects of fragmentation in tropical ecosystems by reducing suitable habitat availability (e.g., Nowakowski et al., 2017; Senior, Hill, González del Pliego, Goode, & Edwards, 2017). When current species distributions do not overlap with the locations of future suitable habitats under climate change (e.g., see Colwell, Brehm, Cardelús, Gilman, & Longino, 2008), populations are likely to decline in landscapes with poor connectivity (Newmark, Jenkins, Pimm, Mcneally, & Halley, 2017). Therefore, effective conservation measures that preserve forest connectivity are needed to support species persistence.

In Southeast Asia, the oil palm, pulp and paper, rubber, and logging industries have driven lowland rainforest clearance (Gaveau et al., 2016; Carlson et al., 2018). As a result, few lowland forests outside of public protected areas remain (Curran et al., 2004). Given the projected growth in palm oil demand (Carrasco, Larrosa, & Edwards, 2014) and governments' interests in the palm oil industry as a vehicle for economic growth (Sayer, Ghazoul, Nelson, & Boedhihartono, 2012), as well as the substantial negative effects of oil palm agriculture on biodiversity (Meijaard et al., 2018), strategies are needed to reduce biodiversity losses in oil palm landscapes (Lucey et al., 2017). Conservation set-asides are one approach used to meet such conservation goals (Green, Cornell, Scharlemann, & Balmford, 2005). To encourage such set-asides, voluntary sustainability certification standards such as the Roundtable on Sustainable Palm Oil (RSPO) require members to identify and conserve areas within plantations that support High Conservation Values (HCVs; Senior, Brown, Villalpando, & Hill, 2015). High Conservation Values are biological, social or cultural values of critical importance that are split into six broad types. Types 1-4 are important environmental values (e.g., for species diversity and ecosystem services), whilst types 5-6 are important for the livelihoods of local communities (e.g., community needs and cultural values) (see Senior et al., 2015, for a full description of HCV types). In the humid tropics, HCV types 1-4 are areas most likely to be forested, and one HCV criterion is that forest areas should be identified and protected if they are important for forest connectivity and/or the preservation of forest corridors.

Previous studies have examined the potential for HCV forest patches to support biodiversity (Lucey et al., 2017), but the contribution of current HCV forest patches to landscape connectivity has not been examined. Here, we meet this research need by evaluating the potential of forests in High Conservation Value Areas (HCVAs) to provide forest connectivity benefits. Our main aims are to: (1) determine the area and distribution of HCVAs in RSPO member-held plantations in Borneo; (2) quantify the amount of 2015 forest cover within these HCVAs; and (3) examine the connectivity benefits of HCVAs for populations with different dispersal abilities. We assess landscape connectivity by using the Incidence Function Model (IFM; Hanski, 1994; Hodgson et al., 2011; Scriven, Hodgson, McClean, & Hill, 2015) to model range expansion of forest-dependent populations across oil palm plantation landscapes. Hence, we define connectivity in our study as landscape colonisation (i.e., the ecological process of range expansion), and so landscapes that are successfully colonised are deemed connected (e.g., see Scriven et al., 2015). We then quantify the connectivity benefits of HCVAs by comparing range expansion rates when HCVAs are simulated to be either present or absent. We test two hypotheses: (1) HCVAs containing more forest that are located in landscapes where HCVAs provide stepping-stone patches generate greater connectivity benefits, and (2) connectivity benefits of HCVAs depend on population dispersal ability and forest cover within the wider landscape.

2. Materials and methods

2.1 HCVA and forest land-cover data

Starting on January 1st, 2010, the RSPO required that all members undertake the New Planting Procedure (NPP; RSPO, 2015), comprising assessments to be conducted prior to new oil palm developments, to prevent new plantings from negatively impacting areas of primary forest, HCV and fragile/marginal soils. Following the NPP assessment, auditors submit a report detailing where new plantings may take place to the RSPO for approval. We obtained the location of HCVAs by digitising HCVA and plantation boundary maps from such NPP audit reports for 70 RSPO member-held plantations in Borneo, including one in Sarawak, Malaysia, and 69 across Kalimantan, Indonesia (Fig. 1; also see Appendix S1 for digitisation details). Around 50% of all 200 NPP assessments published by August 2018 occurred in Borneo (K.M.C., unpublished data, August 2018). Land-cover data (30 m resolution) for 2015 were downloaded from the Atlas of Deforestation and Industrial Plantations in Borneo (https://www.cifor.org/map/atlas/; see Gaveau et al., 2016 for details). We combined intact, logged, and regrowth forest land-cover classes into a single class that we termed ‘forest’, and considered all other land-cover categories as ‘non-forest’. We aggregated these data to 90 m resolution by assigning each larger grid-cell a value representing the number of the nine aggregated 30 m grid-cells that contained forest, so that cell values ranged from zero (0% forest) to nine (100% forest). We chose 90 m resolution to ensure computationally-feasible simulations while ensuring model sensitivity to the small area of HCVAs.

Oil palm plantations often comprise several estates. In our dataset, individual estates within a single NPP assessment (subsequently termed a ‘plantation’) spanned distances of up to ~27 km (Fig. S2). We assessed the area, core area, forest cover in 2015 and placement of HCVAs within these 70 plantations using ArcGIS version 10.4.1. Core area of HCVA patches (spatially discrete areas designated as HCV) was calculated by removing a buffer of 100 m from the edge of each patch (Lucey et al., 2017) (also see Appendix S1 for additional details of geospatial statistics). In addition to HCVAs, many estates contained non-HCVA forest cover within the plantation boundary. This forest could represent areas planned for development, given that oil palm producers undergoing the NPP have lands planned for oil palm plantings but have not yet commenced clearing. Moreover, in Indonesia, national law requires that plantation companies convert all arable concession lands, including currently forested areas, to agriculture (Republic of Indonesia, 2014). Hence, we removed all non-HCVA forest found within the plantation boundaries for our connectivity analyses (823 km^2 across all plantations). This equated to ~8% (823/9884 km^2) of the total plantation area across the 70 plantations. To delimit plantation landscapes for our connectivity analyses and include all separate estates for any given NPP assessment plantation, we considered land-cover within a 30 km radius (the plantation 'landscape') around the centre point (centroid) of each of the 70 plantations (Fig. 2a, Fig. S2). With this size of study landscape, we were able to assess the importance of HCVAs for connectivity in the context of the wider landscape, including habitat beyond the plantation boundary, over distances relevant to the types of species we were modelling.

2.2 Modelling the contribution of HCVAs to forest connectivity using the Incidence Function Model (IFM)

We examined the potential connectivity benefits of HCVAs using a patch-based metapopulation model (Incidence Function Model (IFM); Hanski, 1994). Our measure of connectivity was based on successful range expansion of populations across our 70 plantation landscapes, and we ran separate connectivity models for each plantation. We examined whether forest-dependent populations with a range of dispersal abilities could successfully colonise forest networks within these plantation landscapes over multiple generations (see Hodgson et al., 2011; Scriven et al., 2015). The IFM examines habitat connectivity based on colonisation and extinction dynamics, which are calculated by considering the size of forest patches, the distance to all surrounding forest patches, and species-specific parameters such as dispersal and fecundity (Hanski, 1994) (see Appendix S1 for IFM details).

For each of the 70 plantation landscapes, we simulated range expansion from 'source' to 'target' grid-cells located on opposite sides of the landscape (Fig. 2b; 12 replicates per landscape). All source grid-cells were seeded with full forest cover, regardless of the forest fraction derived from the land-cover data, to prevent source populations from going immediately extinct. Each simulation was terminated once an individual colonised a target grid-cell (a ‘successful’ colonisation; see Fig. 2d), or after 100 generations if no individuals reached the target grid-cell (an ‘unsuccessful’ colonisation; Fig. 2c). Individuals could move across the plantation landscape in any direction but were constrained to reproduce only within forest. We excluded source and target grid-cells over water for six plantations near the coast.

i) Testing connectivity benefits of HCVAs according to the amount of forest they contain

To examine the benefits of HCVAs for forest connectivity, we ran IFMs under three different scenarios, assuming HCVAs were (1) absent and contained no forest cover (‘no forest’), (2) present with current (2015) forest cover (‘current forest’), or (3) present with full (100%) forest cover (‘full forest’). The no forest scenario provides a counterfactual that assumes that without RSPO membership, companies would not conserve HCVAs, but plant these areas with oil palm. The current forest cover scenario represents our best estimate of the current contribution of HCVAs to connectivity. The full forest scenario assumes that all HCVAs are reforested and represents the greatest potential contribution of HCVA designation to connectivity. Since not all HCVAs contain forest or protect biodiversity (e.g., graveyards may be designated because of their cultural value), the full forest cover scenario is likely an overestimate of the benefits of the RSPO for connectivity (see Appendix S1 for further details).

ii). Modelling impacts of dispersal ability on HCVA connectivity

We examined how different assumptions of population dispersal ability affected our measures of forest connectivity, by varying α (alpha), the slope of a negative exponential dispersal kernel within the IFM. This alpha value was inferred by assuming that 5% of individuals within the population could go further than the stated maximum (see Hodgson et al., 2011). We examined five dispersal values corresponding to maximum dispersal distances of 0.5, 1, 3, 5 and 10 km per generation (see Appendix S1). Thus, our model examined different types of populations, ranging from relatively sedentary species (e.g., flightless insects), to relatively mobile vertebrates (e.g., birds or bats). We present results only for population densities of 20 individuals per forested ha (representing winged insects; e.g., see Benedick et al., 2006) because IFM outputs were generally similar when we ran models with alternate population density values (Appendix S1; also see Scriven et al., 2015).

2.3 Analyses of model outputs

We ran connectivity models simulating range expansion across 70 plantations, from 12 different starting locations per planation (Fig. 2b) for three HCVA scenarios and five dispersal abilities (i.e., 15 treatment combinations in a fully-factorial design). We used a Generalised Additive Model (GAM: binomial logistic regression; R package *mgcv*: see Wood, 2011 & Appendix S1 for more details) to examine forest connectivity according to the probability of successful colonisations across 70 plantation landscapes. In this model, the dependent variable was a two-column matrix that represented the number of successful and unsuccessful colonisations across each plantation landscape, from the 12 replicates (Fig. 2b). To prevent each replicate from being treated as independent, we weighted each row of data by the reciprocal of the total number of replicate IFM runs for each plantation (e.g., 1/12). We included dispersal ability and HCVA forest cover scenario as categorical predictor variables. To examine the importance of forest (defined in section 2.1) within the wider landscape on plantation connectivity, our model also included the area of forest cover within each landscape (i.e., outside the focal plantation, but within a 30 km radius of each plantation centre; see Fig. 2a). Finally, we included an interaction between the latitude and longitude of each plantation centre (Wood, 2006). The interaction was fitted as a non-linear (smooth) term selected at an optimal level of complexity by the fitted algorithm. By modelling spatial dependence in the systematic part of the model we were able to account for spatial autocorrelation in the model residuals, determined by inspecting correlograms (see Dormann et al., 2007). We kept all variables in the GAM to examine their relative importance on forest connectivity, and we ran the model using a logit link and binomial errors. To examine the importance of HCVA forest cover scenario, irrespective of dispersal ability, we ran a second GAM without dispersal ability included as a predictor variable, but kept all other model parameters the same. Finally, to examine the robustness of our model outputs, we re-ran the full analysis using a Generalised Linear Mixed Model (GLMM; Appendix S1, Table S1, Fig. S3), but our main conclusions were similar across these two models, and so we only present findings from the GAM analysis in the main text. All statistical analyses were carried out in R version 3.4.0.

3. Results

3.1 Size and amount of forest in HCVAs

The 70 NPP plantations ranged in size from 10 to 547 km^2 (mean = 141, SD ± 81 km^2). In these plantations, on average HCVAs comprised ~12% of the total plantation area (SD ± 10%; ranging from 0.6 to 53%, Fig. 3b). The mean area of individual HCVA patches (N = 1040), was 1.2 km^2 (SD ± 4.4) (Fig. 3c) and on average HCVAs were only about one fifth forested (mean forest cover in HCVAs across the 70 plantations = 21%, SD ± 22%, Fig. 3e). Across all HCVAs, HCV types important for biological diversity and ecosystem services were the most extensive in terms of both area and forest cover, and were present in all plantations (Table S2).

3.2 Connectivity benefits of HCVAs

Connectivity benefits of conservation set-asides

There were few connectivity benefits provided by HCVAs under 2015 forest cover (i.e., ‘current forest’ scenario). Compared to landscapes with no HCVAs (i.e., ‘no forest’ scenario) current HCVAs improved connectivity by only ~3% for all populations (i.e., across all dispersal distances) (Fig. S4, Table S3). When dispersal ability was considered, HCVAs with current forest cover had the greatest relative connectivity benefits for populations with poor dispersal abilities (0.5 km). For these types of species, landscapes with current forest cover in HCVAs were on average 1.2 times better connected than landscapes with no HCVAs, hence a ~20% improvement to connectivity (Fig. 4, Table S4). Nevertheless, since poor dispersers rarely colonised plantation landscapes successfully regardless of HCVA forest cover, the absolute improvement to connectivity was small, increasing from a probability of colonisation success of 0.0095 with no HCVA forest cover to 0.0114 with current forest cover, an overall improvement of just 0.0019 (Fig 4).

Fully reforested HCVAs (i.e., ‘full forest’ scenario) provided greater connectivity benefits than did HCVAs with current forest cover. Overall, irrespective of dispersal ability, the relative improvement to connectivity provided by reforested HCVAs compared to HCVAs with no forest cover was ~16% (Fig. S4, Table S3). When dispersal ability was considered, the greatest percentage improvement to connectivity with HCVA reforestation occurred for populations with poor to intermediate dispersal abilities (Fig. 4, Table S4). Specifically, populations with 0.5, 1 and 3 km dispersal abilities were on average 2.7, 2.4 and 1.2 times more likely to successfully colonise plantation landscapes with full forest cover in HCVAs, compared to landscapes with no HCVAs, respectively (Fig. 4). Despite HCVA reforestation, absolute connectivity benefits were small for the poorest dispersers, as most populations were still unable to successfully colonise plantation landscapes (Fig. 4). These findings were relatively insensitive to variation in population density, although reforested HCVAs may have greater absolute connectivity benefits for the very poorest dispersers if their population densities are high (Appendix S1, Fig. S1). Absolute connectivity benefits following HCVA reforestation were therefore greatest for populations with 1 and 3 km dispersal abilities, for which the probability of successful colonisation increased by 0.13 and 0.16, respectively (Fig. 4). For populations with 5 and 10 km dispersal abilities, both relative and absolute improvements to connectivity were low because the number of successful colonisations was already high (Fig. 4).

3.3 Surrounding forest cover and landscape connectivity

Across all HCVA scenarios, the probability of successfully colonising plantation landscapes increased with dispersal ability and was highest in landscapes with more surrounding forest cover (Figs 4-5, Table S4). For populations with 0.5 km dispersal ability (i.e., representative of very sedentary species) the probability of successful colonisation was relatively low regardless of HCVA scenario, but increased with higher levels of surrounding forest cover (Fig. 5a). Conversely, for populations with 5 to 10 km dispersal abilities (i.e., representative of very mobile species), the probability of successfully colonising plantation landscapes was always high, except for extremely isolated plantations with very low levels (i.e., <100 km^2) of surrounding forest cover (Fig. 5d-e).

4. Discussion

4.1 Characteristics of HCVAs

High Conservation Value Areas in oil palm plantations comprised around 12% of the total plantation area, and so have the potential to make an important contribution to remaining forest cover in oil palm landscapes. Furthermore, almost half of all plantations contained at least one HCVA patch that had a core area larger than 2 km^2 (200 ha), which may provide substantial biodiversity benefits compared to oil palm (Lucey et al., 2017), and have the potential to maintain populations of forest species. Conservation of large tracts of high-quality forest habitat is important for population persistence in human-modified landscapes (e.g., see Edwards, Fisher, & Wilcove, 2012; Lucey et al., 2017), and so small HCVAs may be unable to support viable populations of forest-dependent species unless they are well-connected to other forested areas. However, our results suggest that if well positioned between large tracts of forest, smaller HCVAs may act as ‘stepping stones’ to facilitate movement across fragmented landscapes (Hodgson, Wallis, Krishna, & Cornell, 2016).

HCVAs will provide the largest benefits for both biodiversity and connectivity if they contain high-quality forest (Tawatao et al., 2014; Scriven et al., 2015), but HCVAs in our study were only 21% forested, including intact, logged and regrowth forest. Our estimates of forest cover are likely to be conservative, as they may not include all disturbed and severely burned forest areas (Gaveau et al., 2016), but provide an indication of how much high-quality forest is conserved within HCVAs as of 2015. High Conservation Value Areas identified in plantations before any plantation development activities had commenced (i.e., completely new developments after 2010) contained a higher percentage forest cover than HCVAs in ongoing plantings (Appendix S1 & S3). Nevertheless, across all plantations, forest cover in HCVAs was low, and so there is a pressing need to restore forest habitats within existing HCVAs.

4.2 Benefits of HCVAs for connectivity

Our results suggest that HCVAs currently provide little benefit for connectivity, although landscapes with HCVAs were still up to 1.2 times better connected than landscapes without HCVAs for some populations. Connectivity improved (up to 2.7 times better) for all populations when HCVAs were reforested compared to landscapes with no HCVAs. However, for poor dispersers with very high population densities, connectivity benefits of reforested HCVAs may be even higher (Appendix S1, Fig. S1). As HCV types 5 and 6 are put in place to protect community needs and cultural values rather than biodiversity (see https://www.hcvnetwork.org/), it is likely that these results are somewhat optimistic, as reforestation may not be feasible or support the values that led to HCVA designation. Also, our 'no forest' scenario is not a perfect counterfactual of the benefits of certification, as we do not know how much forest remains in non-RSPO plantations.

We used the IFM (Hanski, 1994) to quantify connectivity because this measure represents a key ecological process (range expansion), which incorporates ecological realism (e.g., metapopulation dynamics) and so produces more ecologically-relevant outcomes compared to simpler approaches. Our results are comparable to those of more standard connectivity metrics (e.g., least-cost models; see Appendix S4), but our IFM approach enables us to examine whether habitat networks of conservation set-asides will allow species to colonise and persist over multiple generations (Hodgson et al., 2011). There is a need to develop modelling approaches that assess the resilience of ecological networks and that go beyond classic landscape connectivity estimates and incorporate ecological outcomes (Isaac et al., 2018). Our approach is therefore an improvement on standard connectivity metrics, but does not include parameters such as reproductive strategy or dispersal phase that are often included in more complex Individual Based Models (IBMs; e.g., see Synes et al., 2015), which are more flexible and predictive than IFMs, but also more computationally intensive. More research is needed to better understand the resilience of habitat networks and identify where connectivity losses are most critical.

4.3. Role of dispersal on connectivity benefits

In landscapes with both current and full forest cover in HCVAs, absolute connectivity benefits were greatest for populations with intermediate dispersal abilities (1-3 km dispersal; representative of fairly mobile species such as forest-dependent butterflies or small sub-canopy birds). Despite high relative connectivity benefits (i.e., percentage improvement), HCVAs provided few absolute connectivity benefits (i.e., change in probability) for extremely sedentary populations, such as weak-flying, insects (e.g., see Malohlava & Bocak, 2010) that disperse less than 0.5 km per generation. These types of species are likely unable to cross non-forest areas, and so may require continuous tracts of forest to move across plantation landscapes. High Conservation Value Areas also provided little connectivity benefit for extremely mobile species dispersing more than 5 km per generation because landscapes are nearly always connected for these species (e.g., large birds or bats; see Corlett, 2009) (Fig. 4). In our connectivity models, we assumed that populations of forest species could leave forested areas and disperse across plantation matrices. In reality, little research has examined the permeability of oil palm plantations for forest-dependent species, which may be confined to forest habitats if they are unable to cross forest-plantation edges (Scriven et al., 2017).

4.4. Influence of the wider landscape on connectivity benefits of HVCAs

The availability of forest in the surrounding landscape varied considerably, and plantations with more surrounding forest were better connected for all types of forest populations. Whilst we did not explicitly explore the relationship between HCVA size and the connectivity benefits of HCVAs, it is likely that even large HCVAs provide little connectivity benefit if they are too isolated from other forested areas in the wider landscape (Fig. S5). Similarly, HCVAs may also provide few additional connectivity benefits if located within reasonably intact landscapes that are already well-connected. High Conservation Value Areas are therefore likely to provide the most connectivity benefits in landscapes with a patchy mix of forest and non-forest areas, dependent on the specific location of HCVAs in relation to surrounding forest (i.e., the intermediate landscape-complexity hypothesis; see Tscharntke et al., 2012) (Fig. S5).

4.5. Conservation implications and recommendations

Almost half of all plantations we studied contained at least one HCVA patch large enough to support forest-dependent species (i.e., with a core area >2 km^2) (Lucey et al., 2017), but these HCVAs may not contain good quality forest, which is needed for maintaining tropical biodiversity (Tawatao et al., 2014). Many of the HCVAs we studied had low forest cover, and we strongly recommend active management by plantation companies to improve forest extent and quality, such as enrichment planting (Yeong, Reynolds, & Hill, 2016). Improving the quality of HCVAs may not only benefit landscape connectivity but also provide important ecosystem services such as pollination (Kormann et al., 2016) and prevention of soil erosion (Dislich et al., 2017). To incentivise oil palm growers to enhance forest quality, we recommend modification of HCV guidance documents and the RSPO's Principles and Criteria (P&C) (see RSPO, 2018) to require restoration of degraded HCVAs. Current RSPO guidelines are not prescriptive about strategies for maximising HCVA connectivity in relation to the wider landscape (e.g., for P&C 7.12; RSPO, 2018). We therefore recommend that if large (i.e., with a core area >2 km^2), isolated HCVAs are identified during HCV assessments, then provision should be made to reconnect these areas via restoration of the intervening plantation matrix. Hence, future revisions to the standard should explicitly ensure that large, isolated HCVAs are reconnected to other tracts of forest such as public protected areas, community-managed forests (Santika et al., 2017), and/or production forests, which can maintain high levels of biodiversity (Edwards et al., 2011).

By May 2019, following 3-4 years of further NPP assessments since our cut-off in 2015, an additional 40 NPP plantations had been assessed in Borneo (https://www.rspo.org/certification/new-planting-procedure/public-consultations). As NPP regulations have remained the same since 2010 (RSPO, 2015) we would not expect any HCVAs within these additional NPP plantations to be different from those in our analyses. Nevertheless, the incorporation of the Assessor Licencing Scheme (ALS) into the NPP in 2015 (see https://hcvnetwork.org/als/) may have had positive impacts on forest connectivity if more forest was designated as HCVA. Additionally, in November 2018, the RSPO revised its P&C and incorporated a zero-deforestation policy (P&C 7.12; RSPO, 2018) via the inclusion of the High Carbon Stock (HCS) approach. The requirement for connectivity is now more implicit in the HCS Approach Toolkit (i.e., via the HCS Forest Patch Analysis Decision Tree) (Rosoman, Sheun, Opal, Anderson, & Trapshah, 2017) and the HCV Common Guidance document (e.g., in relation to HCV 2 for ensuring intact forest landscapes) (Brown, Dudley, Lindhe, Muhtamen & Stewart, 2013). These changes are expected to increase the amount of forest set-aside in new plantings (RSPO, 2018), improving biodiversity (Deere et al., 2018) and connectivity in RSPO-dominated landscapes. We recommend that the RSPO publish digitised maps of HCV/HCS areas, to provide opportunities for maintaining connectivity of HCVAs at landscape scales and facilitate cooperation between neighbouring RSPO member plantations. However, jurisdictional approaches including designation of HCVAs across districts or states (Pacheco, Hospes, & Dermawan, 2017) may be needed to fully realise the potential for linking HCVAs with forest outside the focal plantation. We conclude that improvements to the RSPO standard will likely improve the connectivity benefits of HCVAs, but more research is needed at landscape scales to test these benefits in the long term.

Author's contributions

The specific contributions are as follows: S.A.S., J.K.H., K.M.C. and J.M.L. conceived and designed the research; J.A.H., S.A.S., C.J.M. and J.K.H. conceived and developed the connectivity simulations, which were run by S.A.S. and C.J.M.; K.M.C., S.A.S. and R.H. conceived and oversaw HCVA digitisation; S.A.S. analysed the data, with input from J.A.H., R.H. and C.J.M.; and S.A.S. drafted the manuscript. All authors provided manuscript modifications and gave approval for publication.

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Data availability

Data available via the Dryad Digital Repository: https://doi:10.5061/dryad.600vs50 (Scriven et al., 2019).

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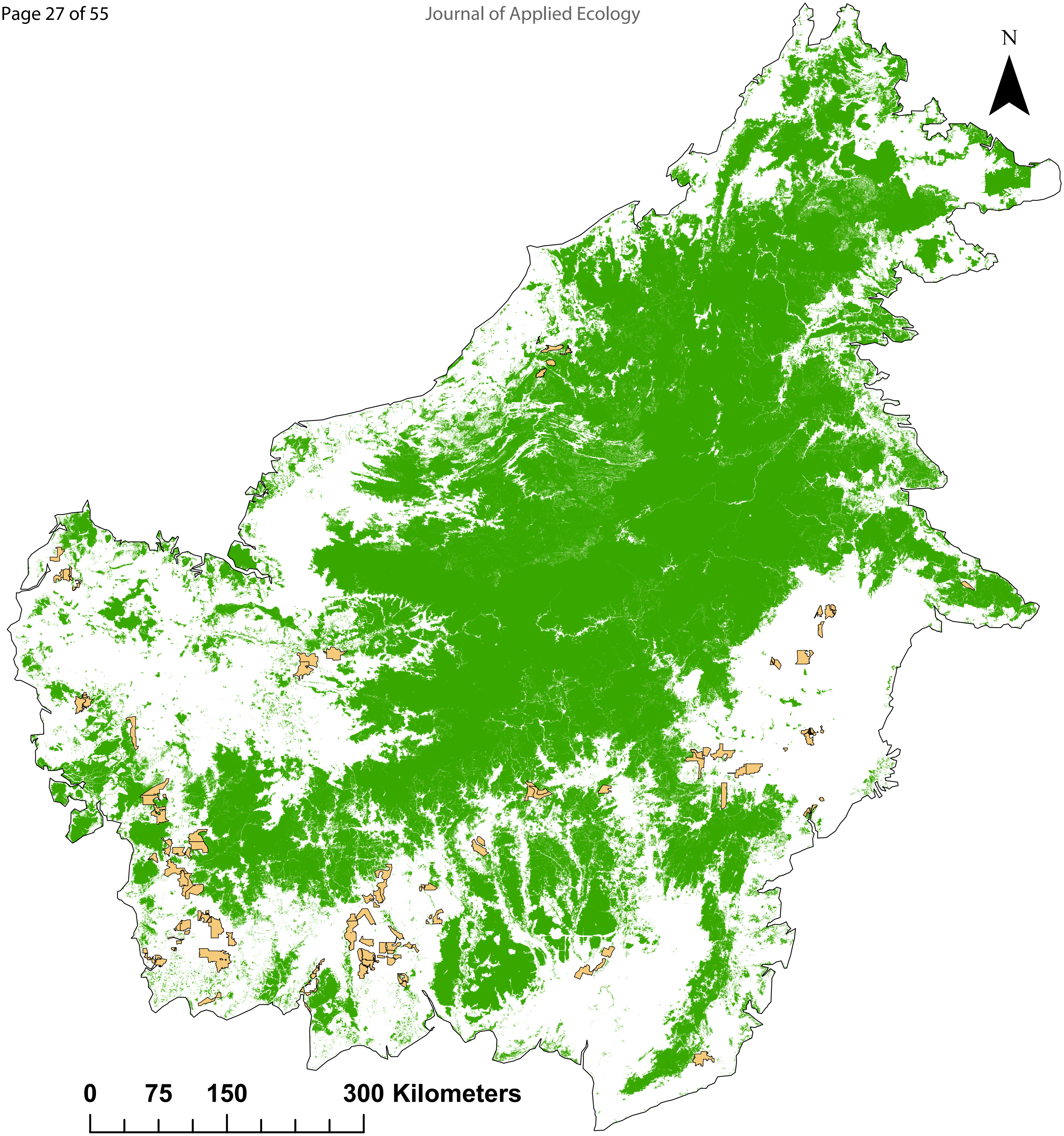
Figure 1. Map of Borneo showing location of 70 New Planting Procedure (NPP) assessment plantations (light orange shading) belonging to 28 RSPO members. Distribution of forest cover (green shading) (30 m grid-cell resolution) represents 2015 intact, logged and regrowth forest according to Gaveau et al. (2016).

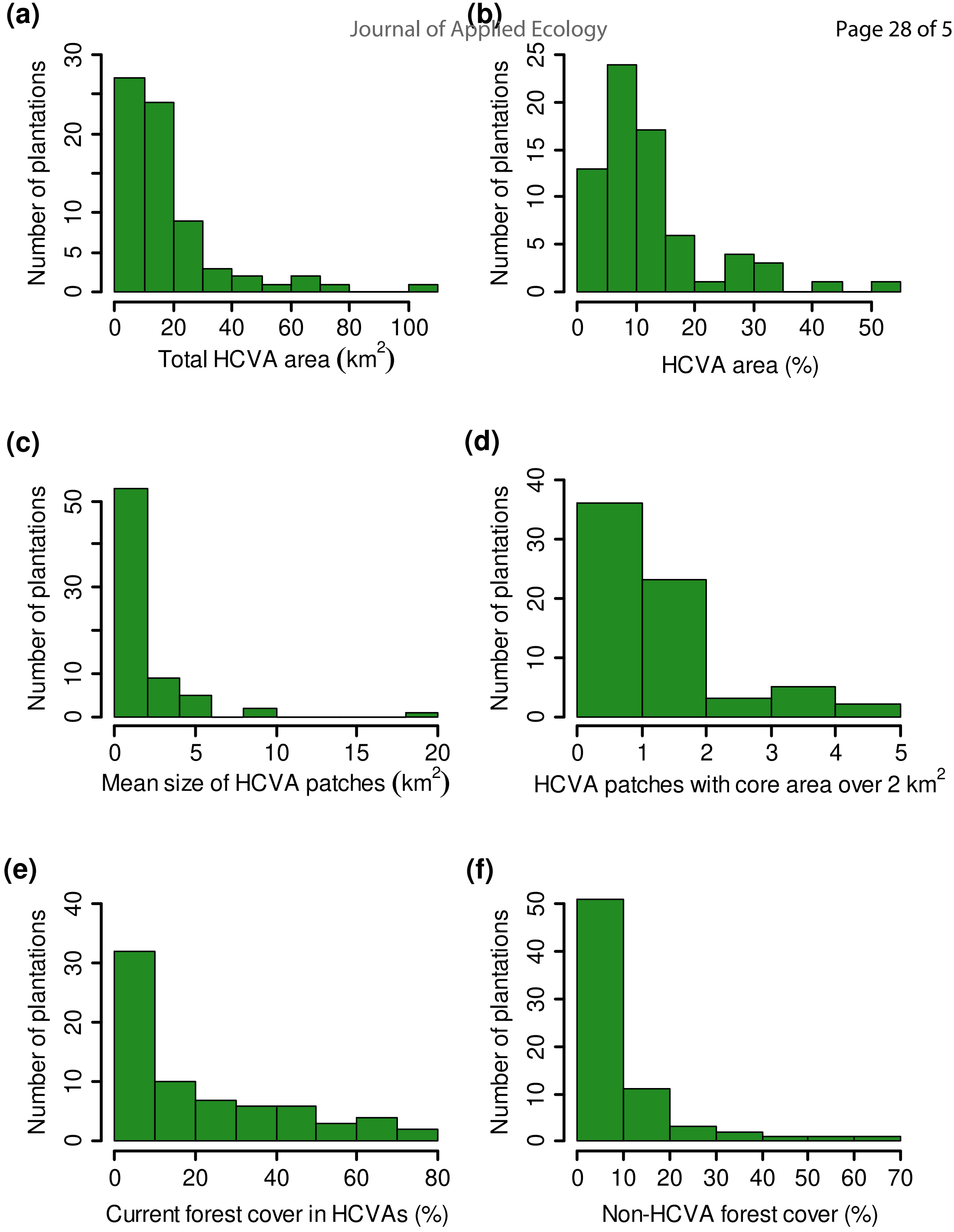
Figure 2. (a) Surrounding forest cover, High Conservation Value Areas (HCVAs) and estate area within a 30 km radius of an exemplar New Planting Procedure (NPP) assessment plantation in Kalimantan (Indonesian Borneo). The centre point (centroid) of the plantation is represented by a yellow circle. (b) An example plantation 'landscape' used to examine the connectivity benefits of HCVAs; numbers represent 12 different starting locations from which 'source' populations were seeded (i.e., forested 90 m grid-cells that were occupied at the start of each simulation). Each source population needed to colonise a forested 'target' grid-cell on the opposite side of the landscape. Hence, source population '2' needed to colonise its target at location '8' in less than 100 generations for the model simulation to be deemed successful. Thus, each number represents a single incidence function model (IFM) simulation, and separate model run for each plantation. (c) Example simulation output whereby populations with 0.5 km dispersal did not colonise the target location within 100 generations (i.e., an 'unsuccessful' colonisation). Colonised grid-cells after 100 generations are shown in grey. (d) Example simulation output whereby populations with 3 km dispersal per generation successfully colonised the target grid-cell within 100 generations (i.e., a 'successful' colonisation). Inset map shows location of property in Kalimantan, Borneo. In this example, the plantation comprised only one spatially discrete estate and no other plantations included in this study fell within 30 km of the focal plantation centroid.

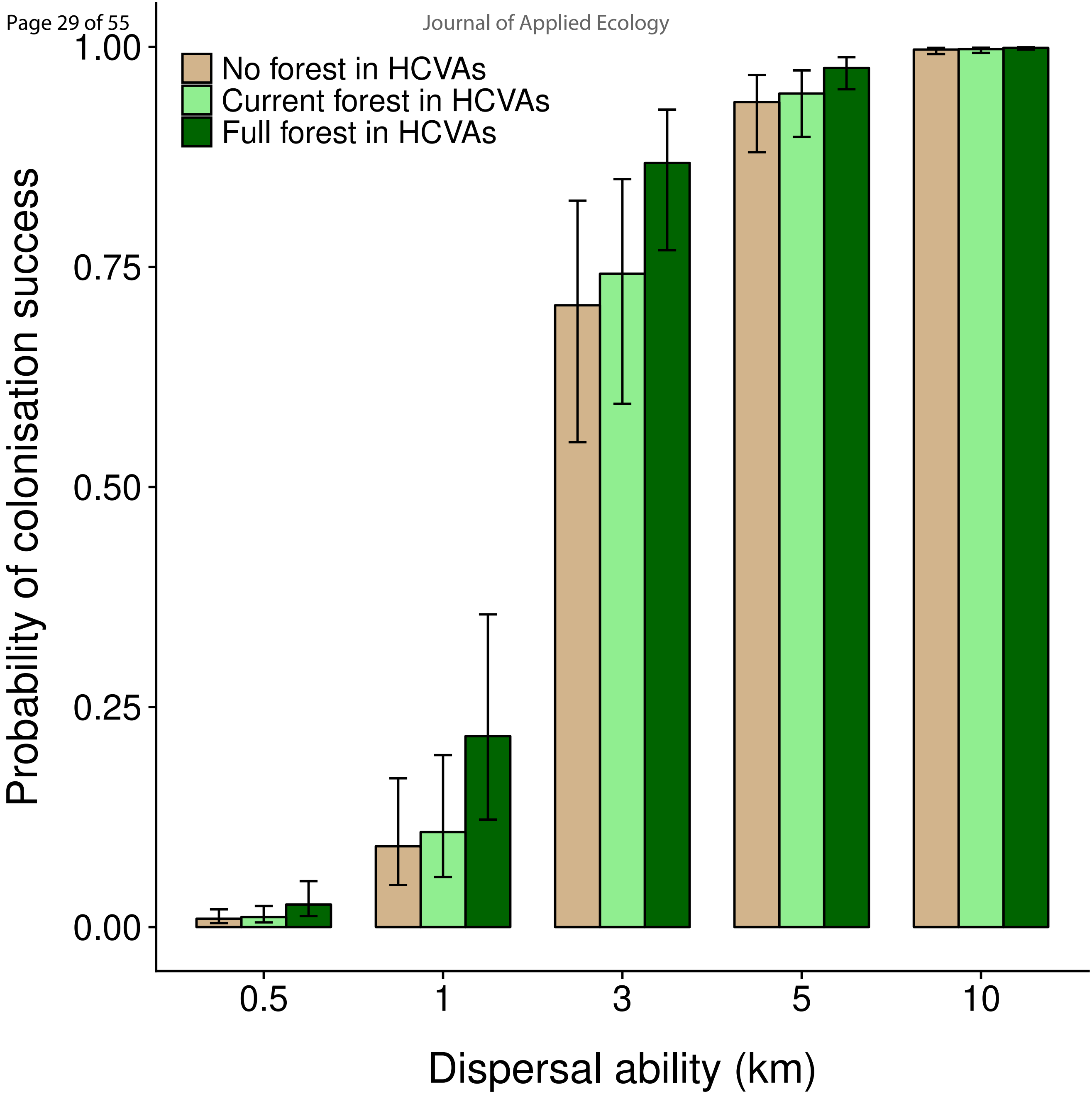
Figure 3. Histograms showing (a) total High Conservation Value Area (HCVA) area (km^2) per plantation, (b) percentage of each plantation deemed HCVA, (c) mean size (km^2) of HCVA patches per plantation, (d) number of HCVA patches with a core area greater than 2 km^2 per plantation, (e) percentage of 2015 forest cover within HCVAs per plantation, and (f) percentage of each plantation covered by non-HCVA forest.

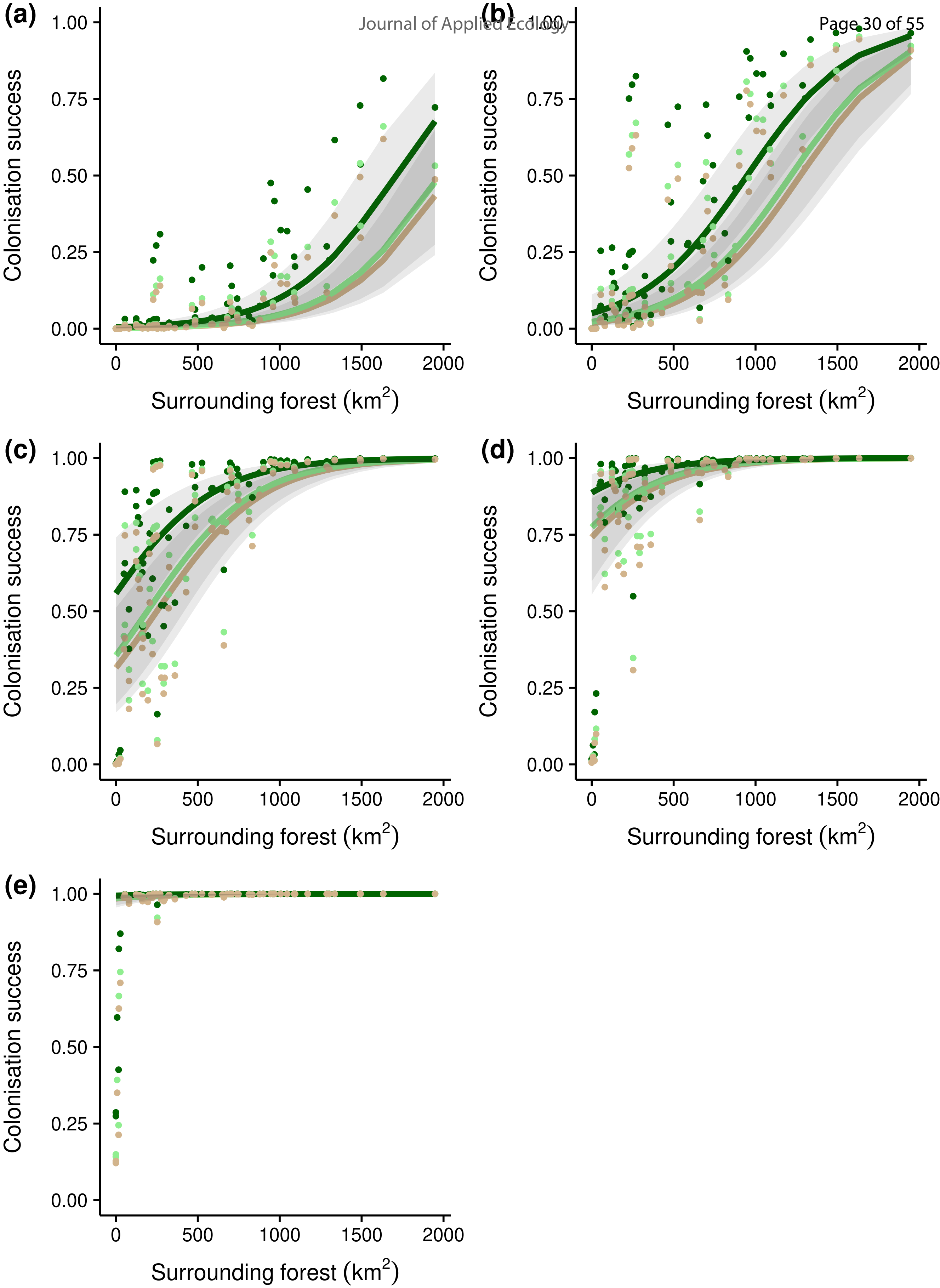
Figure 4. Probabilities of successful colonisation of oil palm landscapes across High Conservation Value Area (HCVA) scenarios for populations with different dispersal abilities: brown shading = no forest cover scenario, light green shading = current (2015) forest cover scenario, and dark green shading = full forest cover scenario. Probabilities are predicted values from the General Additive Model (GAM; binomial logistic regression) where all covariates are held constant (i.e., at their mean values). Bars represent standard errors.

Figure 5. Relationship between the probability of successful colonisation of oil palm landscapes and the area of forest cover surrounding each plantation for populations with (a) 0.5 km, (b) 1 km, (c) 3 km, (d) 5 km and (e) 10 km dispersal abilities. Points and lines are colour coded to represent landscapes with different amounts of forest cover in High Conservation Value Areas (HCVAs; i.e., HCVA scenarios): brown shading = no forest cover, light green shading = current (2015) forest cover, and dark green shading = full forest cover. Points represent predicted values from the General Additive Model (GAM; binomial logistic regression) and lines represent model fit (i.e., when all other predictor variables are at their mean values) for each HCVA scenario. Grey shading represents standard errors around model fit lines.


N
0
75
150
300 Kilometers


(a)
Number of plantations
0
5
10
20
30
0
20
40
60
80
100
Total HCVA area (km²)
(b)
Number of plantations
0
5
10
15
20
25
0
10
20
30
40
50
HCVA area (%)
(c)
Number of plantations
0
10
30
50
0
5
10
15
20
Mean size of HCVA patches (km²)
(d)
Number of plantations
0
10
20
30
40
0
1
2
3
4
5
HCVA patches with core area over 2 km²
(e)
Number of plantations
0
10
20
30
40
0
20
40
60
80
Current forest cover in HCVAs (%)
(f)
Number of plantations
0
10
20
30
40
50
0
10
20
30
40
50
60
70
Non-HCVA forest cover (%)


No forest in HCVAs
Current forest in HCVAs
Full forest in HCVAs
Probability of colonisation success
1.00
0.75
0.50
0.25
0.00
0.5
1
3
5
10
Dispersal ability (km)


(a)
(b)
(c)
(d)
(e)
Colonisation success
1.00
0.75
0.50
0.25
0.00
Surrounding forest (km^2)
0
500
1000
1500
2000

Testing the benefits of conservation set-asides for improved habitat connectivity in tropical agricultural landscapes

Supporting information

Appendix S1. Additional methodological details

Digitisation of High Conservation Value Areas (HCVAs) in New Planting Procedure (NPP) assessment plantations

New Planting Procedure assessments were obtained online from the Roundtable on Sustainable Palm Oil (RSPO) (https://www.rspo.org/) for oil palm growers in Borneo. Maps depicting oil palm plantation boundaries and HCVAs were extracted from these NPP assessments and were georeferenced and digitised in ArcMap version 10.4.1. While RSPO assessment reports for certification may include maps of HCVAs, the quality of these maps is generally insufficient for accurate digitisation. Hence, we focused our connectivity analyses solely on NPP assessments. New Planting Procedure assessment plantations (termed ‘plantations’) included both completely new developments and ongoing plantings. As the RSPO’s NPP was initiated in 2010, completely new developments represent lands slated for land preparation and planting in 2010 or later (i.e., they had not yet been cleared and planted when the assessment was conducted), whilst ongoing plantings represent lands where planting was initiated before 2010. Thus, completely new developments were plantations that contained HCVAs and were identified as part of the NPP process (i.e., that underwent a HCV assessment before development commenced).

We digitised boundaries and HCVAs from 70 randomly-selected NPP assessment reports from 28 RSPO member companies (see Fig. 1 in main text). Where audit report quality was sufficient, we excluded water bodies (i.e., rivers that were classified as HCVAs) from our connectivity analyses. We did this because we were primarily interested in examining the connectivity of terrestrial HCVAs and inclusion of water bodies would overestimate the connectivity benefits of HCVAs in the 'full forest' scenario. These separate features could only be identified when water bodies were large and image quality was high, which meant that the size of the water bodies excised from the HCVA dataset varied. Small streams could often not be distinguished from surrounding riparian HCVAs, and so were included as HCVAs in our analyses. Therefore, in the reforested scenario, such water bodies were converted to forest grid-cells at a 30 m resolution.

Where possible, HCVA polygons were classified by HCV type (e.g., 1 to 6; see https://www.hcvnetwork.org). We included all HCVA types and all HCV management areas in our analyses because HCVA classifications were not available for all plantations. Importantly, HCVAs – including types 5 and 6 – are not always designated for their forest cover. However, inclusion of these HCVA types is unlikely to severely influence our results. First, types 5 and 6 could often not be digitised because of their very small size, so they may be under-represented in our dataset. Second, there are also some instances where these HCVA types may be forested (i.e., for timber extraction, fuel resources, clean water protection and sacred forest sites).

Geospatial statistics:

For each NPP assessment plantation digitised ($N = 70$), we calculated the total area of all HCVAs, the percentage of the total plantation area designated as HCVA, and the percentage forest cover within HCVAs. We also examined the average size of all spatially discrete HCVA patches across plantations and calculated the 'core area' of each HCVA patch. Core area of HCVA patches was calculated by removing a buffer of 100 m, which we assume is the distance over which most edge effects cause detrimental impacts (Laurance et al., 2002), from the edge of each patch (see Lucey et al., 2017). In 44 plantations, information on HCVA type was available, and so we calculated the area and percentage forest cover across different HCVA types for those plantations (Table S2).

The Incidence Function Model (IFM):

The IFM (see Hanski, 1994) is based on the assumptions that (1) extinction probability (i.e., the likelihood that a population goes extinct from any given habitat patch) is inversely related to population size and habitat patch area (i.e., the number of 30 m forest grid-cells within an aggregated 90 m grid-cell), and (2) the probability of patch colonisation is positively related to patch connectivity, whereby the connectivity is a function of the distance to other occupied forest cells and the amount of forest they contain (Hanski, 1994). The connectivity (S_i) of each patch (a spatially discrete forested grid-cell(s)), (*i*), is defined as:

$$A_i \frac{R\alpha^2}{2\pi} \sum_{j \neq i} p_j A_j e^{-\alpha d_{ij}}$$

where A = area of habitat (km^2) in forested grid-cell i or j, R = population density (number of emigrants (individuals) produced per generation per occupied 90 m grid-cell), α = slope of a negative exponential dispersal kernel, p_j = occupancy of j (1 if grid-cell j is occupied, 0 if not) and d_{ij} is the Euclidean distance between the centre of grid-cells i and j. To estimate the carrying capacity of each grid-cell, the amount of forest (i.e., the number of 30 m grid-cells) within each 90 m grid-cell is multiplied by the population density. The extinction probability is subsequently 1/carrying capacity of each 90 m grid-cell at each generation, except within source cells where it was set to zero (see Hodgson et al., 2011, Scriven, Hodgson, McClean, & Hill, 2015, for further details).

Dispersal parameters:

We examined five dispersal values corresponding to maximum dispersal distances of 0.5, 1, 3, 5 and 10 km per generation. The lowest dispersal ability (0.5 km) was chosen to represent an extremely sedentary species such as a flightless, or poor-flying, insect that may require intact forest (e.g., see Malohlava & Bocak, 2010), whilst the intermediate dispersal abilities (1 and 3 km) were chosen to represent fairly mobile species, such as large rainforest butterflies (e.g., see Marchant et al., 2015) or small sub-canopy birds. We also included dispersal abilities that most represent highly mobile populations that can disperse more than 5 km per generation. These are most representative of species such as large birds or bats, which may be able to disperse across large gaps that separate remaining forest habitats (e.g., see Corlett, 2009). We ran our models for 100 generations, a value chosen to allow most populations with poor dispersal ability sufficient time to colonise each landscape assuming it was entirely forested. Hence, colonisation time is a function of the size of the landscape (e.g., 60 km diameter) and the population's dispersal ability (e.g., 0.5 km). Setting a fixed number of generations (rather than years) allowed us to infer the time it would take for different types of 'species' to colonise plantation landscapes. For example, a species with one generation per year would have up to 100 years to colonise the landscape.

Population density parameters:

Our IFM outputs presented in the main text are for populations with 20 individuals per forested ha. However, we ran additional IFMs with population density set much lower and higher than the value in the main text, to 2 and 200 individuals per forested ha. These represent plausible values for different types of species (i.e., mammals with very low population densities and invertebrates with much higher density values) and allowed us to examine the effect of changing this parameter on our findings. We re-ran the IFMs for populations with 0.5 and 3 km dispersal abilities for all our HCVA scenarios. These dispersal distances were chosen specifically because reforestation of HCVAs had the greatest benefit for poor to intermediate dispersers (0.5-3 km per generation), whilst range expansion of highly mobile species was relatively unaffected by habitat loss (i.e., nearly all model simulations were successful for populations with >5 km dispersal abilities; see main text and Fig 4). Hence, we ran additional models for three HCVA scenarios, two population densities and two dispersal treatments (i.e., 12 treatment combinations), for all 70 plantation landscapes (Fig. S1).

For populations with 0.5 km dispersal ability and 2, 20 and 200 individuals per forested ha, landscapes with reforested HCVAs were 1.09, 1.19 and 1.63 times better connected than in landscapes with no HCVAs, respectively, and so reforested HCVAs may have greater connectivity benefits for very poor dispersers with high population densities (Fig. S1). For populations with 3 km dispersal ability and 2, 20 and 200 individuals per forested ha, landscapes with reforested HCVAs were 1.33, 1.25 and 1.19 times better connected than in landscapes with no HCVAs, respectively, and so HCVA benefits were similar across our wide range of population density estimates (Fig. S1). Note that to enable comparison, improvement values presented here were calculated from raw IFM output probabilities and are not predicted probabilities from the GAM, where all covariates were held constant (as presented in the main text). These additional analyses for low and high population densities did not alter our main findings and conclusions, which are robust to different population density parameter values.

Analyses of model outputs:

The statistical relationship between the predictor variables and the probability of successful colonisations across plantation landscapes was modelled using Generalised Additive Models

(GAMs). Generalised Additive Models are a class of statistical regression that allow for non-linear relationships by extending Generalised Linear Models (GLMs) and incorporating a semiparametric 'smooth term'. The complexity of the non-linear relationship for each predictor variable is described by the effective degrees of freedom (edf) of the smooth term, and the form and complexity of the smooth term is a trade-off between the better fit of complex curves and the predictive ability of the model. Hence, the interaction between latitude and longitude (see main text) was selected at an optimal level of complexity, which is a trade-off between goodness of fit and the predictive accuracy of simpler functional relationships (see Wood, 2006; Scroggie & Clemann, 2009 for more details). To examine the robustness of our GAM outputs, we re-ran the same overall analysis using a Generalised Linear Mixed Model (GLMM; binomial logistic regression; R package *lme4*: see Bates, Mächler, Bolker, & Walker, 2015). In this model, the dependent variable was again a two-column matrix that represented the number of successful and unsuccessful colonisations across each plantation landscape, from the 12 replicates (see Fig. 2b in main text), and we included HCVA scenario as a categorical predictor. To ensure that the model converged, we included dispersal ability as a continuous predictor with an orthogonal polynomial transformation. The area of surrounding forest cover within a 30 km radius of the plantation centre was also included as a continuous predictor, but the geographic coordinates (i.e., latitude and longitude) of each plantation centre were not included in the GLMM. Instead, in order to account for spatial autocorrelation in the model residuals, plantations were assigned into 10 clusters (or groups) depending on the specific spatial location of their plantation centroid, and plantation cluster was included as a random factor in the model. Plantation identity (i.e., a unique number between 1-70 assigned to each plantation) was subsequently nested within cluster. We kept all variables in the GLMM, to examine their relative importance on connectivity, and we ran the model using a logit link and binomial errors.

Model outputs were comparable with the results of the GAM analysis presented in the main text (see Table S1 for model coefficients and Fig. S3 for output probabilities of successful colonisations across HCVA scenarios and dispersal abilities).

Table S1. Outputs from the Generalised Linear Mixed Model (GLMM; binomial logistic regression) determining the effects of dispersal ability (*N* = 5), High Conservation Value Area (HCVA) forest cover scenario (*N* = 3) and amount of surrounding forest cover (km^2) on the probability of successful colonisation for 70 plantation landscapes.

Random effects	**Variance**	**SE**		
Plantation ID: Plantation cluster	0.4057	1.401		
Plantation cluster	3.877	1.969		
Fixed effects	**Estimate**	**SE**	***z* value**	***P***
Intercept	0.4057	0.6674	0.61	0.543
HCVA Scenario 2 (current forest)	0.1992	0.08564	2.33	0.020
HCVA Scenario 3 (full forest)	1.112	0.08832	12.59	<0.0001
poly (Dispersal, 2) 1	121.2	3.321	36.48	<0.0001
poly (Dispersal, 2) 2	-36.65	1.844	-19.87	<0.0001
Surrounding forest (km^2)	2.420	0.2284	10.60	<0.0001

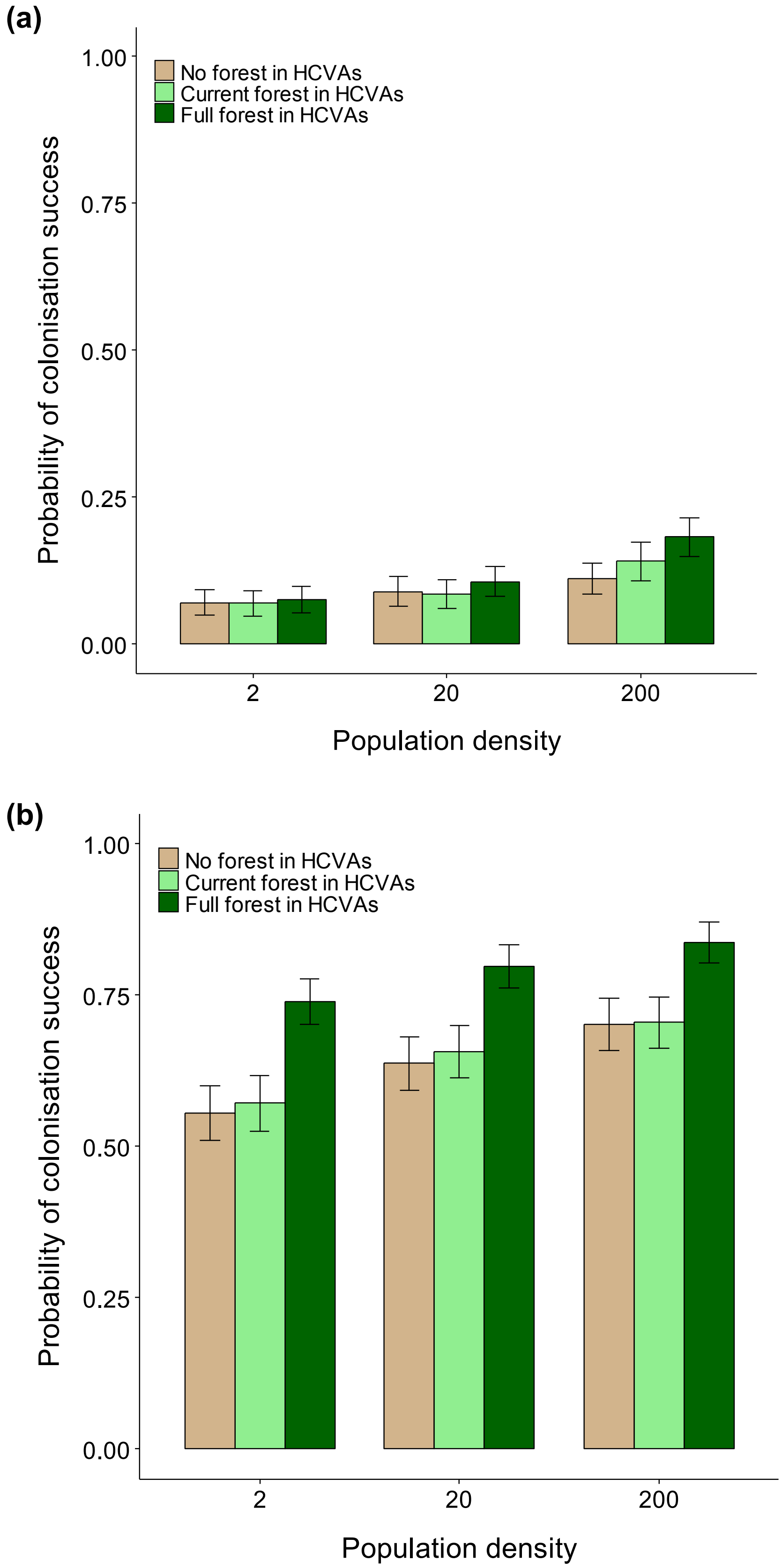

(a)
1.00
0.75
0.50
0.25
0.00
Probability of colonisation success
No forest in HCVAs
Current forest in HCVAs
Full forest in HCVAs
2
20
200
Population density
(b)
1.00
0.75
0.50
0.25
0.00
Probability of colonisation success
No forest in HCVAs
Current forest in HCVAs
Full forest in HCVAs
2
20
200
Population density

Figure S1. Probabilities of successful colonisation of oil palm landscapes across High Conservation Value Area (HCVA) scenarios for populations with different population densities (representing the number of individuals per forested ha). Brown shading = no forest cover scenario, light green shading = current (2015) forest cover scenario, and dark green shading = full forest cover scenario, for (a) 0.5 km and (b) 3 km dispersal abilities. Probabilities are calculated from raw data and bars represent standard errors.

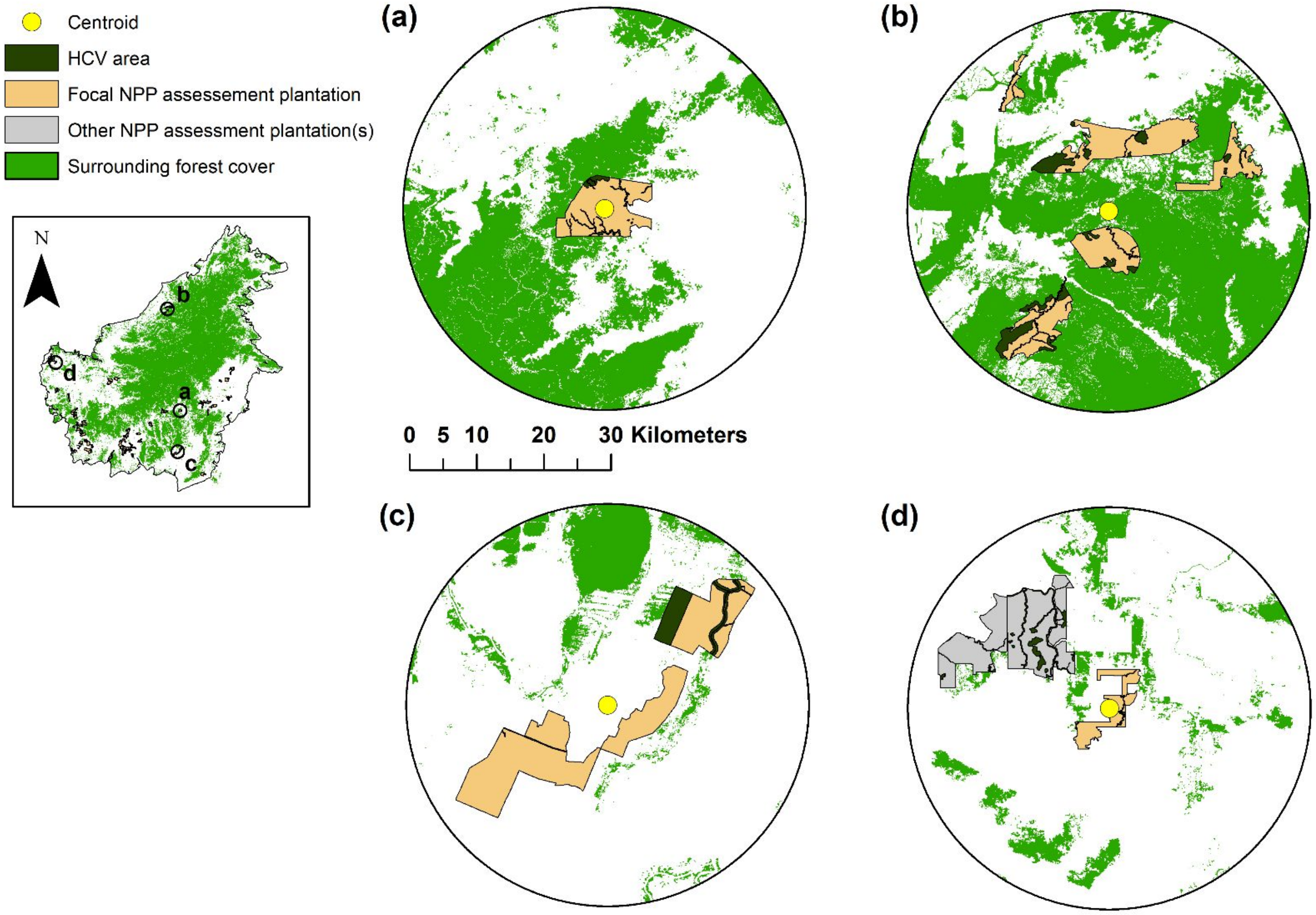


Figure S2. Surrounding forest cover, High Conservation Value Areas (HCVAs) and estate area within 30 km of example New Planting Procedure (NPP) assessment plantations. The centre point (centroid) of the plantation is represented by a yellow circle. New Planting Procedure assessment plantation examples comprise: (a) one single estate, (b) and (c) multiple estates, and (d) one single estate that falls within 30 km of other NPP assessment plantation estates. These plantation 'landscapes' were used to examine the connectivity benefits of HCVAs (see Fig. 2 in main text for further details).

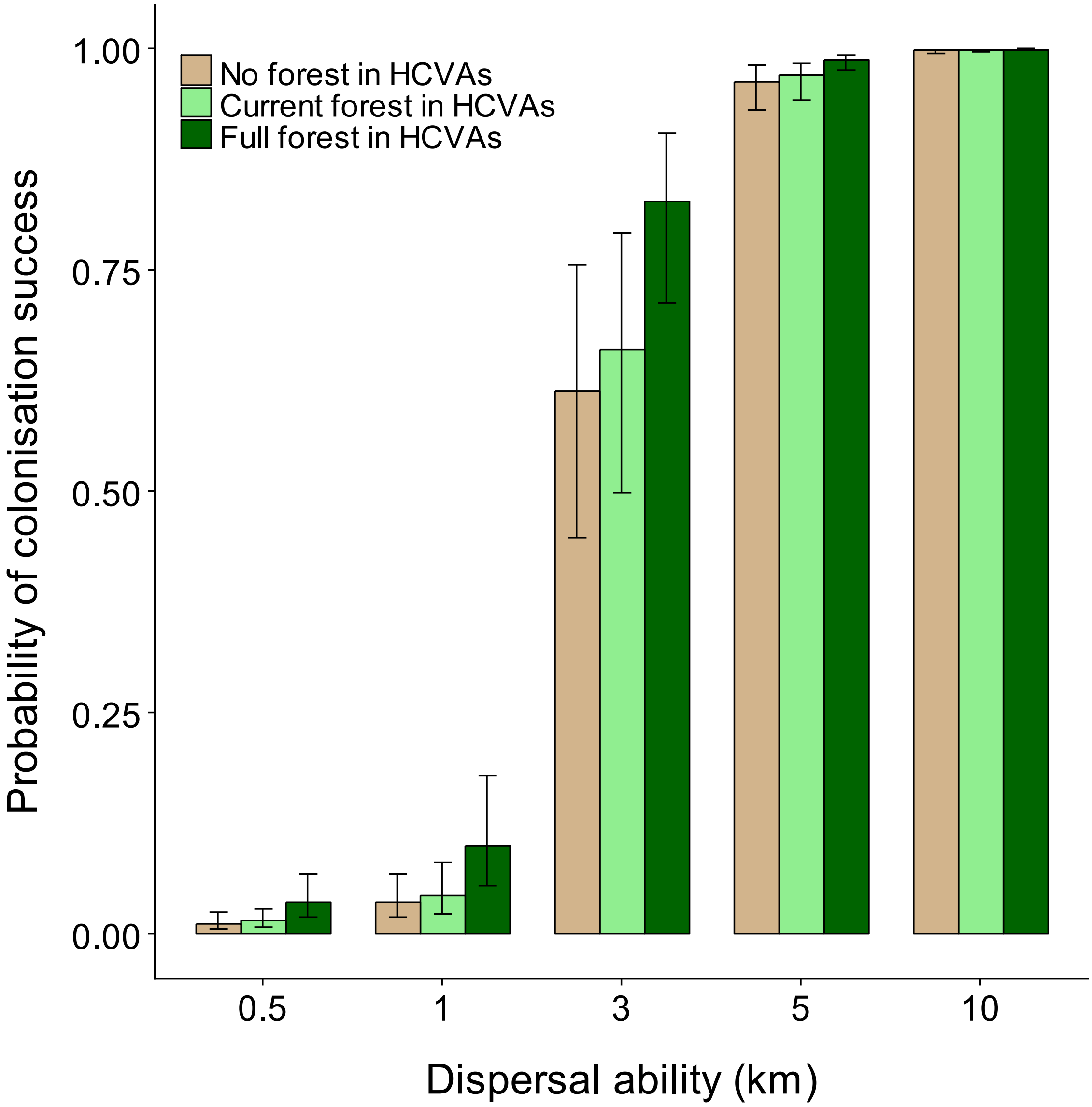


Figure S3. Probabilities of successful colonisation of oil palm landscapes across High Conservation Value Area (HCVA) scenarios for populations with different dispersal abilities: brown shading = no forest cover scenario, light green shading = current (2015) forest cover scenario, and dark green shading = full forest cover scenario. Probabilities are predicted values from the Generalised Linear Mixed Model (GLMM; binomial logistic regression) where all covariates are held constant (i.e., at their mean values). Bars represent standard errors for fixed effect uncertainty.

Appendix S2. Additional results

Table S2. Summary statistics and standard deviation (SD) calculated for different types of High Conservation Value Areas (HCVAs) across Roundtable on Sustainable Palm Oil (RSPO) New Planting Procedure (NPP) assessment plantations in Borneo.

HCVA type	Number of plantations with HCVAs present (%) (*N* = 70)	Average total HCVA area (km^2) across plantations (*N* = 44)[b]	Total HCVA area (km^2) across plantations (*N* = 44)[b]	Average forest cover (%) across plantations (*N* = 44)[bc]
1: Species diversity	100	12.6 (± 12.4)	553	26 (± 28)
2: Landscape-level ecosystems	49	3.6 (± 8.2)	159	27 (± 30)
3: Ecosystems and habitats	49	5.6 (± 15.5)	248	31 (± 35)
4: Critical ecosystem services	100	15.5 (± 19.3)	682	21 (± 23)
5: Community needs	47[a]	2.8 (± 6.3)	122	19 (± 23)
6: Cultural values	50[a]	1.5 (± 5.3)	67	15 (± 22)

[a] The number of plantations containing HCVA types 5 and 6 may be underestimated, as these areas could often not be digitised because of their small size. These areas can represent sacred trees, graveyards, wells or other small features that are important for local communities.

[b] These values have been calculated across the 44 plantations for which HCVAs could be classified by type. Note that many HCVAs are of more than one type and so occur across multiple categories; hence values are not additive.

[C] Forest cover derived from Gaveau et al. (2016).

Table S3. Outputs from the General Additive Model (GAM; binomial logistic regression) determining the effects of High Conservation Value Area (HCVA) forest cover scenario (*N* = 3) and amount of surrounding forest cover (km^2) on the probability of successful colonisation for 70 plantation landscapes.

Parametric (linear) terms	**Estimate**	**SE**	***z* value**	***P***
Intercept	-0.5230	0.1876	-2.787	0.0053
HCVA Scenario 2 (current forest)	0.0631	0.1659	0.381	0.7034
HCVA Scenario 3 (full forest)	0.357	0.1683	2.122	0.0339
Surrounding forest (km^2)	0.0013	0.0003	4.822	<0.0001
Smoothed (non-linear) terms	**edf**	**Ref.df**	**Chi.sq**	***P***
Latitude, Longitude (interaction)	15.69	19.98	61.72	<0.0001

Table S4. Outputs from the General Additive Model (GAM; binomial logistic regression) determining the effects of dispersal ability (*N* = 5), High Conservation Value Areas (HCVA) forest cover scenario (*N* = 3) and amount of surrounding forest cover (km^2) on the probability of successful colonisation for 70 plantation landscapes.

Parametric (linear) terms	**Estimate**	**SE**	***z* value**	***P***
Intercept	-6.196	0.6004	-10.32	<0.0001
HCVA Scenario 2 (current forest)	0.1796	0.2799	0.642	0.5211
HCVA Scenario 3 (full forest)	1.007	0.2887	3.488	<0.0001
Dispersal (1 km)	2.353	0.3809	6.176	<0.0001
Dispersal (3 km)	5.522	0.475	11.62	<0.0001
Dispersal (5 km)	7.348	0.557	13.19	<0.0001
Dispersal (10 km)	10.45	0.910	11.48	<0.0001
Surrounding forest (km^2)	0.003	0.0006	4.989	<0.0001
Smoothed (non-linear) terms	**edf**	**Ref.df**	**Chi.sq**	***P***
Latitude, Longitude (interaction)	21.75	25.85	112.8	<0.0001

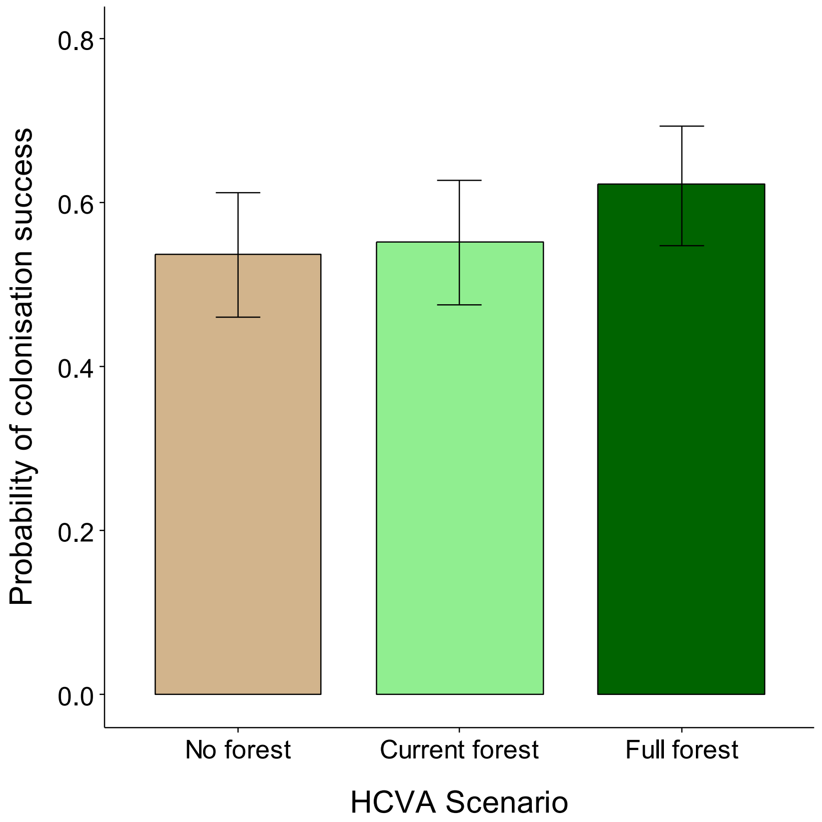
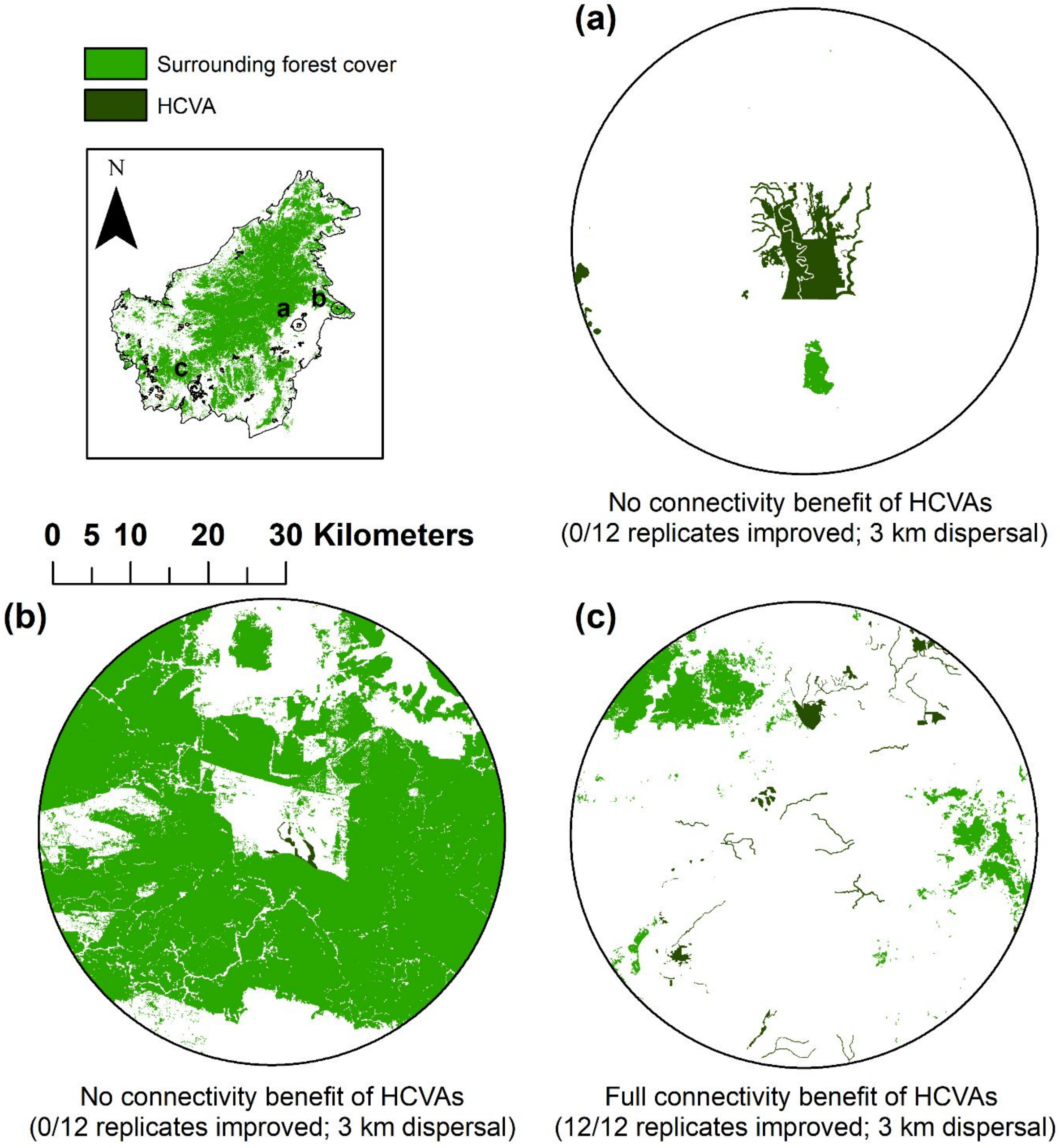


Figure S4. Probabilities of successful colonisation of oil palm landscapes across High Conservation Value Area (HCVA) scenarios: brown shading = no forest cover scenario, light green shading = current (2015) forest cover scenario, and dark green shading = full forest cover scenario. Probabilities are predicted values from the Generalised Additive Model (GAM; binomial logistic regression) where all covariates are held constant (i.e., at their mean values) and where dispersal abilty was excluded from the model. Bars represent standard errors.



No connectivity benefit of HCVAs (0/12 replicates improved; 3 km dispersal)

No connectivity benefit of HCVAs (0/12 replicates improved; 3 km dispersal)

Full connectivity benefit of HCVAs (12/12 replicates improved; 3 km dispersal)

Figure S5. Example plantation landscapes used to test the connectivity benefits of High Conservation Value Areas (HCVAs) using an incidence function model (IFM). Modelled landscapes are centred on New Planting Procedure (NPP) assessment plantations. Scenario (a) reflects an oil palm landscape where full forest cover in HCVAs (dark green shading) made little improvement to landscape connectivity, due to lack of forest cover surrounding the plantation (light green shading). Scenario (b) also reflects a landscape whereby full forest cover within HCVAs made little improvement to landscape connectivity, due to the large

amount of surrounding forest cover and the relatively small HCVA area. Whilst scenario (c) reflects a landscape whereby full forest cover in HCVAs had large connectivity benefits for certain forest populations.

Appendix S3. Examining the differences in total HCVA area and forest cover between completely new developments and ongoing plantings.

Methods:

To determine differences in total HCVA area (km^2) and forest cover between completely new developments and ongoing plantings, we compared the percentage of total plantation area that was designated as HCV across completely new developments (i.e., planted following the NPP assessment; $N = 23$) and ongoing plantings (developed before 2010; $N = 47$), and compared percentage forest cover of HCVAs across these plantation types. We also calculated the percentage of the total plantation area that comprised non-HCVA forest. As data did not follow a normal distribution, we compared differences in the total HCVA area (km^2) and the percentage forest cover within HCVAs in new developments and ongoing plantings using a Mann-Whitney U test. Additionally, we also used a Mann-Whitney U test to compare the percentage of total plantation area that contained non-HCVA forest between new developments and ongoing plantings.

Results:

The average percentage of total plantation area designated as HCVA was similar for completely new developments (12%; $N = 23$) and ongoing plantings (12%; $N = 47$) ($W= 530$; $P = 0.90$). However, HCVAs in new developments contained significantly more forest than those that were part of ongoing plantings (27% versus 18%, respectively) ($W= 702$; $P = 0.04$). New developments also contained a higher percentage of non-HCVA forest compared to ongoing plantings (14% versus 6%, respectively), but this difference was marginally insignificant ($W= 68.2.5$; $P = 0.08$).

Appendix S4. Examining the connectivity benefits of HCVAs using least-cost models.

Methods:

To determine whether the connectivity benefits of HCVAs were robust to our metric of connectivity, we calculated least-cost paths (e.g., see Adriaensen et al., 2003) across each of the 70 plantation landscapes and for the three different HCVA scenarios: assuming HCVAs were (1) absent and contained no forest cover (‘no forest’), (2) present with current (2015) forest cover (‘current forest’), or (3) present with full (100%) forest cover (‘full forest’), using the standard GRASS GIS (version 7.4) *r.cost* function. The *r.cost* function is based on a least-cost path algorithm (see GRASS Development Team, 2019 for details) and calculates the cumulative cost of moving between geographic locations (e.g., source and target grid-cells) on an input raster whose grid-cell values represent cost. We created two different resistance surface scenarios (30 m resolution raster grids) in which: (1) forest grid-cells were given a resistance (cost) value of one and non-forest (matrix) grid-cells were given a resistance value of 100, and (2) forest grid-cells were given a value of zero and non-forest grid-cells were given a resistance value of one. Hence, in resistance scenario 1, the cost of traversing a non-forest grid-cell was 100 times greater than traversing a forest grid-cell. For each of the 70 plantation landscapes, we calculated least-cost paths for six directions across each landscape (i.e., directions 1-6 in Fig. 2b), and recorded the overall cost of each least-cost path (i.e., the sum of resistance values of the grid-cells along the path). Resistance scenario 1 was chosen as it would likely yield a high level of variation between our 70 plantations landscapes, whilst scenario 2 was chosen as the final cost value represented the number of 30 m matrix grid-cells that must be traversed across the least-cost path between the source and target grid-cells. We then compared the overall least-cost distance values across all plantation landscapes to determine whether HCVA scenario affected the overall cost.

Results:

For resistance scenario 1 (where forest grid-cells were given a resistance value of one and non-forest (matrix) grid-cells were given a resistance value of 100), the cost of crossing plantation landscapes with no HCVAs (i.e., 'no forest' scenario) was 1.02 (92004/89861; ~2.4%) and 1.26 (92004/72856; ~26%) times more than landscapes with HCVAs that contained current forest cover ('current forest' scenario) and full forest cover ('full forest' scenario), respectively (Fig. S6a). Results were similar for resistance scenario 2 (where forest grid-cells were given a value of zero and non-forest grid-cells were given a resistance value of one) (Fig. S6b). Least-cost model results are comparable to the overall average results of the IFM (averaging over dispersal distances) whereby landscapes with current forest cover in HCVAs were 2.4% better connected than landscapes with no HCVAs, and landscapes with reforested HCVAs were 13.2% better connected. Note that to enable comparison, improvement values presented here were calculated from raw IFM output probabilities and are not predicted probabilities from the GAM, where all covariates were held constant (as presented in the main text). Overall, the relative improvement of reforesting HCVAs compared to landscapes with no HCVAs is slightly greater when least-cost values are the chosen metric of connectivity. Similarity of results is to be expected because both metrics are affected by the total amount of habitat in the landscape, and its spatial arrangement. For reference, across all landscapes the full forest scenario contained 3.3% (1233/37371 km^2; area of forest in HCVAs in the full forest scenario/total landscape forest area) more forest than the no forest scenario, and the current forest scenario contained 0.72% (268/37371 km^2; area of forest in HCVAs in the current forest scenario/total landscape forest area) more forest. The fact that relative improvements in connectivity are more substantial than relative improvements in forest cover underlines the importance of considering how landscapes function, even when limited information is available to parameterise models.

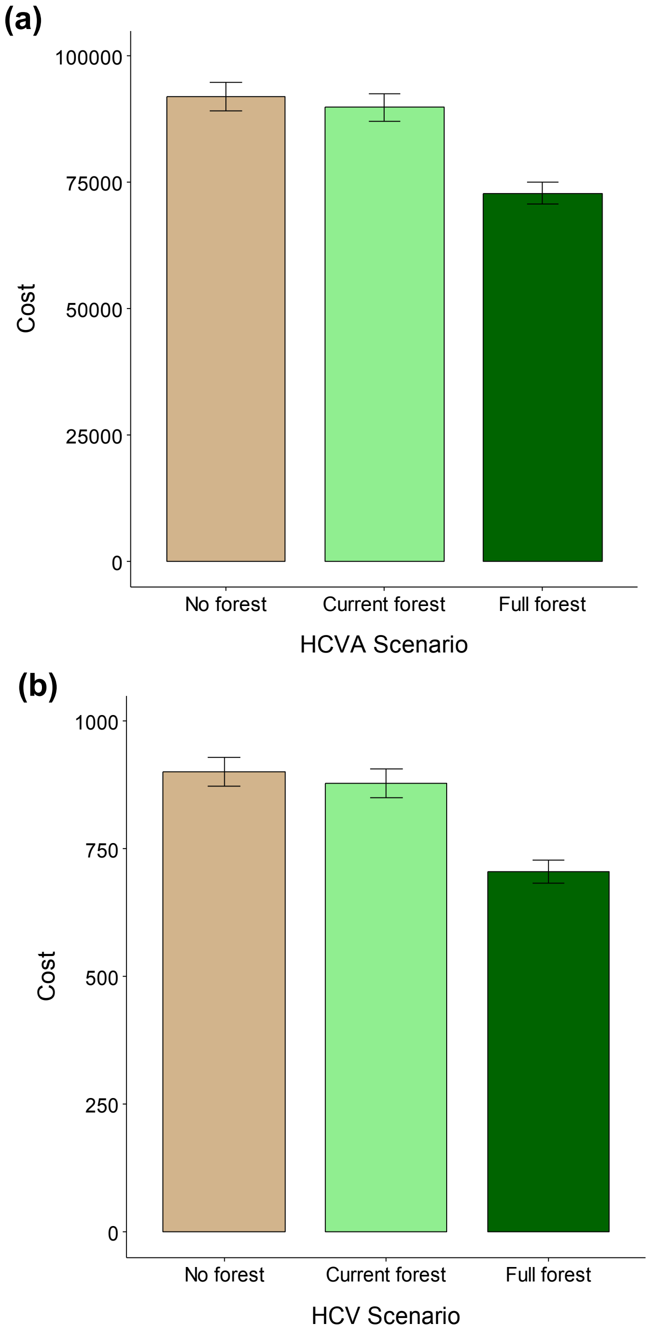


Figure S6. Cost values produced by least-cost models run for different HCVA scenarios: brown shading = no forest cover scenario, light green shading = current (2015) forest cover scenario, and dark green shading = full forest cover scenario, and for two different resistance scenarios. In (a) (resistance scenario 1) forest grid-cells were given a resistance value of one and non-forest (matrix) grid-cells were given a resistance value of 100. In (b) (resistance scenario 2) forest grid-cells were given a value of zero and non-forest grid-cells were given a resistance value of one. Bars represent standard errors.

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Caption for graphical abstract:

Forested High Conservation Value Area (HCVA) within a Roundtable on Sustainable Palm Oil (RSPO) certified oil palm plantation in Borneo. We found that HCVAs in Borneo currently provide few connectivity benefits because on average they contain only 21% forest cover. However, if these conservation set-asides are fully reforested, plantation landscapes could be up to 2.7 times better connected than landscapes with no HCVAs for some forest species. Photo credit: Robin Hayward.