Year: 2011

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DOI: https://doi.org/10.1098/rstb.2011.0049

Originally published at:
Ewers, R M; Didham, R K; Fahrig, L; Ferraz, G; Hector, A; Holt, R D; Kapos, V; Reynolds, G; Sinun, W; Snaddon, J L; Turner, E C (2011). A large-scale forest fragmentation experiment: the stability of altered forest ecosystems project. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1582):3292-3302.
DOI: https://doi.org/10.1098/rstb.2011.0049

A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project

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Running header: The SAFE Project

Abstract

Opportunities to conduct large-scale field experiments are rare, but provide a unique prospect to reveal the complex processes that operate within natural ecosystems. Here, we review the design of existing, large-scale forest fragmentation experiments. Based on this review, we develop a design for the Stability of Altered Forest Ecosystems (SAFE) Project, a new forest fragmentation experiment to be located in the lowland tropical forests of Borneo (Sabah, Malaysia). SAFE represents an advance on existing experiments in that it: (1) allows discrimination of the effects of landscape-level forest cover from patch-level processes; (2) is designed to facilitate the unification of a wide range of data types collected on ecological patterns and processes that operate over a wide range of spatial scales; (3) has greater replication than existing experiments; (4) incorporates an experimental manipulation of riparian corridors; and (5) embeds the experimentally fragmented landscape within a wider gradient of land use intensity than existing projects. The SAFE Project represents an opportunity for ecologists across

disciplines to participate in a large initiative designed to generate a broad understanding of the ecological impacts of tropical forest modification.

Keywords: Biological Dynamics of Forest Fragments Project; Calling Lake Fragmentation Experiment; deforestation; hierarchical sampling design; Savannah River Site Corridor Experiment; Wog Wog Habitat Fragmentation Experiment

1. INTRODUCTION

Habitat fragmentation is one of the central issues in conservation biology [1] and has been a source of considerable scientific debate since the early application of island biogeography theory [2] to terrestrial habitat islands and the design of nature reserves [3-4]. These debates led directly to the establishment of the Minimum Critical Size of Ecosystems experiment in the Brazilian Amazon [5-6], now known as the Biological Dynamics of Forest Fragments Project (BDFFP). This visionary experiment has probably had the single greatest impact on the general understanding of the ecological impact of forest fragmentation and is routinely cited in the conservation literature around the world [7-8].

The BDFFP heralded a new approach to the study of habitat fragmentation, lifting it from one based almost solely on observational studies, to one based on experimentation. The implications for scientific advancement were tremendous: the use of statistically based before-after-control-impact sampling provides much stronger inference than observational studies relying on a space-for-time substitution to act as a control [9].

Since the establishment of the BDFFP, there have been at least 20 more experimental tests of habitat fragmentation [10], based mostly in grasslands or fields, but just one of these has matched the BDFFP in terms of the size and number of fragments [11].

Large-scale experiments may be the only way to determine the responses of forest systems to global change [12]. They generate results that are comparable to those arising from observational studies [13] which ensures that large-scale experiments have real-world practical relevance. However, the opportunities for large-scale, replicated and controlled landscape experiments are rare. When they are undertaken, they are invariably time-consuming and costly to establish, and consequently there will always be a premium placed on maximising the long-term scientific pay-off from this initial investment. Consequently, any such experiments should address a wide range of ecological questions [10]. Moreover, just as the BDFFP was designed to address a central, policy-relevant issue about reserve design, it is incumbent upon researchers establishing new fragmentation projects to ensure that they address not only policy questions that are relevant at the time of project establishment, but also for the foreseeable future.

Focusing on four large-scale forest fragmentation experiments located on three different continents, we summarise the key features of existing experimental designs and assess their ability to address emerging issues in landscape ecology. Based on this review, we develop and scrutinise the design for the Stability of Altered Forest Ecosystems (SAFE) Project, a new rainforest fragmentation experiment being established in the wet tropical forests of Malaysian Borneo.

2. AN OVERVIEW OF EXPERIMENTAL DESIGNS FOR FOREST FRAGMENTATION STUDIES

Habitat area is probably the single most influential variable that can be manipulated in a fragmentation experiment, and has formed the backbone of the designs at the BDFFP, the Calling Lake Fragmentation Experiment, and the Wog Wog Habitat Fragmentation Experiments. All three experiments used replicates of a small number of fragment size categories, rather than opting for a more extensive, continuous gradient of unreplicated fragment sizes. In all cases, fragment sizes were distributed on a log-scale. The BDFFP initially planned four size categories on a $\log_{10}$ scale (10^0, 10^1, 10^2 and 10^3 ha), but the largest of these was never isolated. Calling Lake followed a similar design, but added an intermediate fragment size of 40 ha. Wog Wog, however, had a much smaller forest area available for the experiment and used fragment sizes of 0.25, 0.875 and 3.062 ha.

Surprisingly, given the island biogeography framework on which these experiments were initially designed, isolation (or conversely connectivity) has seldom been built into large scale fragmentation experiments. Only the Savannah River Site Corridor Experiment has manipulated isolation distances, with fragments separated from each other by distances of 64 to 384 m [14]. Two other experiments used a coarser approach to manipulate isolation by introducing a 'connected' versus 'isolated' treatment [11, 15]. A second experiment at the Savannah River site was focused around issues of fragment connectivity, with connected *vs* unconnected patches forming the central basis of the experimental design [15]. Calling Lake also addressed connectivity in this manner, with connected fragments cleared on just three of the four sides leaving the fragment directly connected to continuous forest [11]. The unconnected fragments at Calling Lake are separated by a fixed distance of 200 m from continuous forest, which is similar to the average (but variable) distance of isolation at the BDFFP. By contrast, the fragments at Wog Wog are as close as 50 m to each other and approximately the same distance from continuous forest [16]. Forest regeneration in the matrix habitat at the BDFFP has allowed inadvertent tests of connectivity, in that matrix regrowth has connected fragments to the surrounding continuous forest over time [17].

The potential for ecological patterns to be obscured by environmental variability means that the replication and spatial interspersion of fragments that differ in area should be maximised [16] All four forest fragmentation projects used a blocked experimental design and a similar number of replicate fragments per block to allow for this. However, the scale of landscape manipulations is often constrained by land availability, as well as fiscal and logistical considerations, setting a limit on the amount of replication that can be practicably achieved. Savanna River employed five or six replicate blocks (a total of 27 and 30 fragments) for the two experiments respectively, Wog Wog employed four replicate blocks of fragments (a total of 12 fragments), whereas the BDFFP (11 fragments) and Calling Lake (12 isolated and 8 connected fragments) both used three blocks. However, the Calling Lake landscape required that one of the blocks have a 100-ha fragment that is widely separated from the others, and blocks in the BDFFP likewise vary in terms of the number and size range of fragments: Dimona (2×1-ha, 1×10-ha and

1×100-ha fragments), Porto Alegre (1×1-ha, 1×10-ha and 1×100 ha fragments) and Esteio (2×1-ha and 2×10-ha fragments).

2.1 Emerging questions in landscape ecology and the ability of existing experiments to address them

Most early habitat fragmentation studies focussed on patch-level patterns and processes such as area, isolation and edge effects. These analyses typically ignored the wider landscape context within which the fragments themselves were embedded. The ongoing coupling of fragments to a surrounding landscape, which contains its own distinct community and suite of ecosystem processes, provides a generic source of differences from the expectations of fragments as true 'islands', surrounded by a matrix that is solely viewed as a barrier to dispersal. One problem that has thus emerged recently in analyses of fragmentation studies is that the patterns these early studies were ascribing to patch variables may have been confounded due to strong correlations between the patch variables and total amount of habitat area in the landscape [18-19]. Unless duly considered, observed fragmentation impacts could then, in some cases, be incorrectly attributed to patch rather than landscape variables. There can be no doubt that reducing the amount of forest in a landscape will have direct impacts on biodiversity, but very few studies have carefully teased apart the effects of habitat amount from the effects of the spatial configuration of that habitat [19]. Rigorously testing the relative impacts of area and configuration is challenging and requires identification of paired landscapes of the same size and with the same total amount of habitat, but with distinctively different habitat configurations.

A related issue revolves around the relative importance of forest cover patterns that are measured at the scale of a single fragment, vs. those that are measured at the scale of a landscape. Donovan et al. [20] provided one of the first simultaneous analyses of patch and landscape features and found that edge effects (a patch-level pattern) varied according to the amount of forest in the surrounding landscape, and landscape-scale effects have also been documented in some fragmentation experiments [21]. Mensurative fragmentation studies now routinely incorporate data on both patch- and landscape-level forest cover patterns, but none of the existing forest fragmentation experiments have explicitly included landscape forest cover in their designs. To date, the only experiments incorporating such a landscape-scale design feature have been conducted at small spatial scales such as the fractal grass and sand mosaic landscapes generated by With et al. [22].

Another feature of fragmented environments that has not yet been subjected to a direct controlled experimental test is the effect of the surrounding habitat matrix. Fragmentation reviews have stressed for two decades that the matrix may be the strongest determinant of within-fragment conditions [23-25], and these conclusions have recently been supported by a meta-analysis of the responses of more than 1 000 species to habitat area and isolation [26]. However, actual experimental manipulation of the matrix habitat poses a formidable challenge for a forest fragmentation experiment. All three large-scale fragmentation experiments created fragments that are embedded within a single land use type. Of these, only the BDFFP has been able to test for matrix effects as a *post-hoc* by-product of land abandonment by the cattle ranchers who manage the matrix surrounding the experimental fragments, rather than as an *a priori* component of the experimental design [17, 27]. At the BDFFP, the initial conversion of forest to cattle pasture that created the fragments was partly supported by government subsidies, but the ranches that were established proved to be unprofitable and were subsequently abandoned. Consequently, the matrix at the BDFFP can now be divided into three categories: cattle pasture, *Vismia* regrowth on abandoned pastures that were burned, and *Cecropia* regrowth on abandoned pastures that were not burned [28].

3. OPPORTUNITIES AND CONSTRAINTS FOR THE SAFE PROJECT

The influence of landscape-level forest cover on the ecological patterns and processes within individual fragments has not yet been subjected to a large-scale experimental test, but will play a central part in the Stability of Altered Forest Ecosystems (SAFE) Project. SAFE will be based in Malaysian Borneo, where the Royal Society South East Asian Rainforest Research Programme (SEARRP, www.searrp.org) has a long-standing relationship with the Sabah Foundation (Yayasan Sabah, www.ysnet.org.my), a state government body charged with spearheading the socio-economic development of the Malaysian state of Sabah. As part of this role, the Sabah Foundation is converting a portion of their forestry estate to oil palm plantation, creating an opportunity for a large-scale deforestation and forest fragmentation experiment. The forest that will be converted has, like most of the forest in the region, already undergone two rounds of selective logging (Table 1). The Sabah Foundation, in collaboration with its subsidiary company Benta Wawasan and with the Sabah Forestry Department, set the time frame of the plantation development such that forest conversion will occur in 2011, giving an opportunity to collect pre-fragmentation data. The long collaborative history between the Sabah Foundation and SEARRP, combined with the high profitability of palm oil [29], work together to ensure the long-term persistence of the experimental fragments that the SAFE Project will create.

In total, the entire SAFE Project experimental site has an area of 7200 ha. The experimental site currently connects a Virgin Jungle Reserve (VJR) of 2200 ha to a large area of forest (> 1 million ha). Most of the large expanse has been through either one or two rotations of selective logging, although it also encompasses three large conservation areas that have never been logged (Danum Valley, Maliau Basin and Imbak Canyon). The VJR will become isolated during the conversion process. Within the experimental block, the Sabah Foundation agreed to allow up to 800 ha of cultivatable land to be set aside as forest fragments. In addition to this allowance, Malaysian law prohibits the clearance of forest on steep slopes and along permanent streams, accounting for another approximately 500 ha (~7 % of the experimental area). The size of the experimental area, combined with the land that is legally prohibited from clearance and the amount of land that can be retained for experimental purposes makes it feasible to place fragments in locations that will vary in the amount of forest cover in the landscapes surrounding them. This provides a unique opportunity to assess in a controlled, experimental design the impact of landscape context on a wide range of ecological dynamics in forest fragments.

We stress that the SAFE Project is not the cause of deforestation in this landscape. Rather, it will be embedded within an independent establishment of a large oil palm plantation in a lowland dipterocarp rainforest. The project is located in an area that has been gazetted for conversion to plantation for the last 20 years, and will use a planned and government approved oil palm conversion to conduct a large-scale landscape experiment. As such, the SAFE Project is using an opportunity that has arisen from the expansion of the oil palm industry to establish an experiment that can simultaneously address basic scientific questions, the answers to which should be important for forest management and conservation in tropical Asia.

3.1 Requirements for the SAFE experimental design

Large-scale experiments must meet the needs of multiple users, both now and in the future. Here, we outline a set of four criteria that the experimental design needs to conform to in order to meet this requirement.

1. For any experiment, it is important to have a relatively standard design that generates well-replicated data in a transparent and open manner. This enables researchers to employ well-established statistical methods that produce unambiguous results and inferences while still allowing supplementary analyses.
2. The BDFFP experience shows that, over the lifetime of a long-term experiment, research teams investigate a wide range of ecological patterns and processes that vary in the spatial scales over which they operate. It is difficult to predict the range of questions and taxa that will ultimately be studied over the long haul of a landscape experiment. But regardless of the details, to obtain maximum benefit from having multiple teams investigating multiple phenomena at a given site, the layout of the experiment and the placement of sampling points need to be designed so as to allow

the investigation of ecological phenomena across varying spatial scales. The design should allow for data on those various phenomena to be tied together, allowing linkages among them to be subjected to statistical analyses. This mandates a form of hierarchically structured, multilevel spatial design for the fragments and the sampling points within them.

3. As an experiment, it will be possible to collect pre-fragmentation data, which greatly increases the power of any analysis. However, as happened at the BDFFP, it is likely that many researchers will only begin to use the SAFE fragments once they have been created. Because these researchers will have no opportunity to collect pre-fragmentation data, it is vital to ensure that the spatial layout of the experiment also permits the use of appropriate spatial controls, as are commonly used in observational studies. Control sites should be located as close as possible to the experimental fragments, yet be located as far as logistically feasible from forest edges. The location of forest control sites does, however, need to be traded off against the logistical difficulties of accessing those sites.
4. Environmental variation can become a major source of experimental error [16]. Consequently, the design should control for obvious and known gradients in environmental variation, such as altitude and slope. Aspect is a less important issue for tropical studies than it is for temperate studies, where there can be substantial differences in biological patterns on north vs south facing slopes [30-31].

4. A FRACTAL SAMPLING DESIGN FOR UNIFYING DATA ACROSS SPATIAL SCALES

We suggest that it is possible to meet the first two criteria presented above by employing a hierarchical sampling design based around a triangular fractal pattern (Fig. 1), and extending that design to define the placement of fragments. To our knowledge, fractal sampling designs have not been used in prior experimental landscape studies, and in general are still scant in empirical ecological investigations.

Triangles were chosen as three sampling points is the minimum required to generate multiple estimates of point-to-point turnover in community composition (ß diversity), allowing researchers to estimate the mean and variance of ß diversity at a given distance. The distance between sample points at the finest scale of the fractal is determined by a desire to ensure the results from this project are comparable to those of the BDFFP. The distances from the edge to interior of circular fragments of size 1, 10 and 100 ha are respectively $10^{1.75}$, $10^{2.25}$ and $10^{2.75}$ m. Consequently, the 1^{st}-order base of the fractal consists of equilateral triangles with sides of 56 m ($10^{1.75}$) and a sampling point at each vertex. These 1^{st}-order fractals will be placed so that the centroids of the triangles are located on the vertices of a 2^{nd}-order fractal consisting of an equilateral triangle with 178 m sides ($10^{2.25}$). The 2^{nd}-order fractals will be embedded within 3^{rd}- and 4^{th}-order fractals with sides of 564 and 1780 m ($10^{2.75}$ and $10^{3.25}$) respectively (Fig. 1). Consequently, one 4^{th}-order fractal comprises 81 sampling points which are separated by distances distributed evenly along a $\log_{10}$-scale, providing a total of 81, 243, 729 and 2187 pairwise combinations of traps separated by mean distances of $10^{1.75}$, $10^{2.25}$, $10^{2.75}$ and $10^{3.25}$ m respectively (Fig. 1a).

This sampling design provides a clearly defined structure for aggregating data on ecological phenomena that vary over different spatial scales, paving the way for the unification of data collected on different components of the ecosystem. Ecological patterns that are expected to vary over fine spatial scales, such as microclimate or soil microbial composition, could be sampled at the vertices of the 1^{st}-order fractals. Tree and large mammal communities, by contrast, should vary over larger spatial scales and could be sampled at the vertices of the 2^{nd} or higher-order fractals. At each of the 2^{nd}-order vertices, data collected at the three vertices of the 1^{st}-order fractal could either be aggregated to scale up the data to the same spatial scale as the variables measured at the 2^{nd}-order fractal, or treated as pseudo-replicates of 1^{st}-order phenomena.

5. THE SAFE PROJECT EXPERIMENTAL DESIGN

5.1 Experimental forest fragmentation

The fractal sampling pattern will be used to define the physical location of fragments, with the series of distances used to separate sampling points in the control sites replicated within and among the experimental fragments. The SAFE Project will be a split-plot experiment comprising six replicate blocks (A-F in Fig. 2), each containing four plots with samples in either 4 × 1-ha fragments, 2 × 10-ha fragments, 1 × 100-ha fragment, or in pre-fragmentation continuous forest that will be converted to oil palm (i.e. matrix samples). Each of the six blocks thus contains seven fragments in three size treatments, giving a total of 42 experimental fragments (total area = 744 ha). To be directly comparable with the BDFFP, SAFE will create fragments of 1, 10 and 100 ha. This range of fragment sizes is also very relevant to policy decisions about land-use change, as the real-world distribution of fragment sizes typically results in more than 90 % of fragments being 100 ha or smaller [32-33]. However, fragments in the SAFE Project will be circular, thereby minimising the edge:area ratio of fragments. This differs from the square plots used at previous forest fragmentation experiments, and ensures the negative impacts of edge effects will be kept to a minimum in this experiment.

Fragments within plots are located to ensure that there is (1) equal sampling effort across plot size classes and (2) an equal spatial distribution of sampling effort in the four plots (Fig. 1), analogous to the design of the Kansas Fragmentation Study [34]. Plots with fragments will be separated by 178 m ($10^{2.25}$ m). The fourth plot with the matrix samples will be aligned with the 100-ha fragment to create a large, 1128 m edge gradient extending from the centre of the fragment, across the fragment edge and out into the matrix. The spatial distribution of sampling points within and among fragments is based on a transect derived from the fractal sampling scheme used in the continuous habitat controls (Fig. 1), ensuring that the distances among samples in the fragments and controls are directly comparable.

The six experimental blocks are placed within the experimental site in a non-random manner in such a way as to maximise the range of forest cover that will remain in the landscapes surrounding sampling points. Average forest cover around sampling points within the six blocks ranges from 16 to 50 % when a landscape is described as a circle with a 3 km radius (Table 2). Experimental blocks are also oriented within the study area in a non-random manner to take advantage of the local topography, such that sampling transects run at roughly equal altitude. Finally, blocks are also oriented to remove or minimise other potentially confounding effects such as slope, latitude, longitude, and distance to forest edges prior to the forest conversion (see analyses below).

In addition to the sampling sites in the control habitats and experimental fragments, SAFE will take advantage of a 2200 ha Virgin Jungle Reserve that will become isolated during the forest conversion process (Fig. 2). A single transect of sampling points will be placed from the edge to interior of the VJR. The transect extends more than twice the distance of the transects in the experimental fragments, representing the larger size of the VJR, but the distribution of sampling points is still based on the fractal pattern used elsewhere. A similar, long transect will be placed from the edge to interior of the continuous logged forest habitat.

5.2 Control sites and the forest modification gradient

One 4th-order fractal sampling network will be established in each of three control habitats; continuous old growth forest, continuous logged forest and continuous oil palm plantation. Taken together, the control habitats and experimental fragments represent a comprehensive gradient of habitat modification comprising (1) old growth rainforest, (2) logged rainforest, (3) logged and fragmented rainforest, and (4) intensive agriculture in the form of an oil palm plantation. Moreover, each of these levels of habitat modification incorporate different land use and disturbance intensities (Table 1). For example, in the old growth forest sites, located in the Maliau Basin Conservation Area, one of the 3rd order groups of sampling points is located in the water catchment of the Maliau Basin

Field Centre (OG3 on Fig. 1). This water catchment was lightly logged in the 1970s and again in the mid-1990s to provide timber for the field centre, but the vertical structure and species composition of the canopy and undergrowth communities in this area remain representative of primary forest in the wider region. Similarly, the six blocks of experimental fragments vary in the level of logging damage and in the amount of forest cover surrounding them, and the oil palm control sites vary in the age and canopy cover of the palms. The forest modification gradient that is built into the SAFE experimental design mimics the real-world pattern of habitat conversion in Borneo, ensuring that phenomena observed in the study should be directly pertinent to policy issues in the region.

5.3 Experimental variation of riparian corridors

Many tropical nations now have environmental legislation prohibiting the clearance of forest along the banks of streams and rivers. In Malaysia, the legal requirement is for a 30 m strip of forest to be left standing on either side of streams with permanent above-ground water flows. Legislation of this type is designed primarily to protect water quality, and has the added benefit of preserving wildlife corridors connecting standing forest remnants. SAFE will experimentally manipulate the width of riparian corridors to examine their efficacy and with a view to identifying the optimum width for future land use conversions (Fig. 2).

We identified six micro-watersheds within the experimental area that have approximately equal area (260 ha ± SD 10) and slope (16˚ ± SD 2). Watersheds of this size contain headwater streams that are approximately 2 km long. The six watersheds vary in the amount of forest cover that will remain following conversion to oil palm (range 3-30 %; forest cover estimates include the experimental fragments). Each experimental watershed has been assigned one of six riparian widths (0, 5, 15, 30, 60, and 120 m on each side of the stream), with the widths assigned in a way that ensures log-transformed width is not confounded with watershed size ($r_4 = 0.28$, $P = 0.60$), average watershed slope ($r_4 = -0.05$, $P = 0.93$) or forest cover ($r_4 = 0.64$, $P = 0.17$). The permanent streams in the experimental watersheds are small (2 – 3 m across), and are typically enclosed by the forest canopy which meets over the stream. Consequently, from a biodiversity corridors perspective, the range of corridor widths is two times that of the riparian widths (0 – 240 m).

In addition to the experimental watersheds, we have identified three control watersheds (1 × old growth forest, 1 × logged forest and 1 × oil palm plantation). Control watersheds were chosen to match the experimental watersheds as closely as possible in terms of size and slope.

5.4 Analyses of potential confounding factors within the SAFE experimental design

We conducted a series of analyses to ensure that the spatial design of the SAFE experiment will not be confounded with known physical features of the environment. All validation analyses were based on the 2nd-order fractal, meaning that the groups of three sampling points separated by 56 m were represented by a single datapoint. This was because the GIS data used in these analyses are on a 60 m grid, so 1st-order sampling points often fell within the same grid-square and do not represent separate points for analysis. We modelled the effect of fragment size, transect order (distance along the transect within a plot; Fig. 1), and their interaction on a set of variables that could potentially confound future analyses: (1) latitude and longitude; (2) altitude; (3), slope; (4) pre-fragmentation land use context, represented by distance to forest edges prior to the forest conversion; and (5) isolation, represented by distance to large forest areas following forest conversion (we defined large forest areas as the VJR and the continuous area of logged forest to the north of the experimental area: the VJR is included because much of it has not been logged, and because it is a large area of forest in which temporal changes and species losses are expected to be very slow). Fragment size and transect order were both modelled as categorical variables, with transect order taking the values 1–4 for sample points extending from the centre to the extremity of each plot (Fig. 1). Matrix samples were included in the analysis, and coded as having a fragment 'area' of 0 ha. The split-plot experimental design imposes a hierarchical sampling structure on the data, so effects were tested using mixed effects models [35-36] with *p*-values estimated on the basis of Markov Chain Monte Carlo samples (function *aovlmer.fnc* in the R package 'languageR' [37]). All analyses were conducted using the 'lme4' [38] and 'languageR' [37]packages for R.2.12.1 software [39], and the results are summarised in Table 3.

When the location of blocks is accounted for, our analyses show that there should be no significant confounding of latitude with fragment area, transect order or the area × transect interaction. Moreover, the main effects of fragment area, transect order or the area × transect interaction will not be confounded with altitude, slope, distance to pre-fragmentation land use or isolation (Table 3).

Mean altitude at sampling points across the experimental blocks is 450 m (median = 460 m, interquartile range 72 m), and mean altitude within blocks ranges from a minimum of 400 m (Block B) to a maximum of 470 m (Block F). Altitude is partially confounded with landscape forest cover: when forest cover is estimated at the 3-, 4- and 5-km scales, there is a strong, negative correlation with altitude ($r < -0.80$, $P < 0.001$). These correlations are driven by the lower altitude of Block B and are not significant if that block is removed from the analysis. Altitude and forest cover at smaller spatial scales are also confounded, although the correlation is not significant ($|r| < 0.53$, $P > 0.27$).

The location of sampling points with respect to pre-fragmentation land use is of concern, as edge effects that are already impacting the experimental area may alter ecological patterns detected in the pre-fragmentation data, reducing the likely impact that experimental habitat fragmentation would have had, compared to a uniform landscape. Experimental blocks will vary in their distance from the pre-fragmentation forest edges, with mean distances ranging from 910 m (Block C) to 2680 m (Block B). All sampling points will be at least 585 m from the pre-fragmentation edges and 87 % of sampling points will be more than 1 km away, which is beyond the expected penetration distance of most edge effects, as found in the BDFFP [8]. As with distance to pre-fragmentation forest edges, the experimental blocks will vary in their isolation distance to large forest areas, with mean isolation distances ranging from 870 m (Block D) to 3130 m (Block C).

5.5 Forest cover in the landscape surrounding experimental blocks

We considered the proportion of the landscape that will remain forested around an individual sampling point following the experimental fragmentation to be landscape forest cover. Blocks will vary significantly in the average amount of landscape forest cover at the four largest spatial scales tested (Table 2a). Blocks D and F are located such that forest cover shows little variation at any spatial scale (33-36 % and 31-34 % respectively), whereas forest cover at Block B increases from 36 % at 1 km scale to almost 60 % at 5 km scale. Across all experimental blocks, forest cover at any spatial scale is tightly correlated with forest cover at similar scales, but that correlation weakens as the difference in spatial scales increases (Table 2c).

Proportion forest cover in the landscape will be strongly confounded with distance of isolation from large forest areas, with significant correlations existing between isolation distance and forest cover at all spatial scales, and particularly strongly for the 2- and 3-km landscapes ($r < -0.75$, $P < 0.001$ for both correlations). Such correlations are almost inescapable in landscape experiments, and suggest that isolation from large forest areas and landscape forest cover are different metrics reflecting the same landscape-scale gradient in forest cover [19].

6. DISCUSSION

Opportunities to design and implement large-scale, long-term ecosystem experiments are rare, but may provide an important method to assess the impacts of global change on ecosystems [12]. The present-day research and policy environment requires a detailed understanding of the effects of habitat modification on the ability of tropical forests to deliver ecosystem services, such as carbon sequestration and the maintenance of water supplies, and to support the high levels of biodiversity for which they are renowned [7]. Consequently, there is a definable need to establish a new, large-scale forest fragmentation experiment which can address a new generation of research and policy questions. Locating such an experiment in a region undergoing heavy logging and rapid conversion to high-intensity agricultural systems, and designing the experiment to mimic the sequence of land use change and the types of habitats that are being generated by economic forces in the region, ensures that such a project will have direct relevance to high-profile policy issues. Here, we have presented the design for the Stability of Altered Forest Ecosystems Project which is being established in the lowland dipterocarp forests of Malaysian Borneo. Most such experiments have been carried out in temperate or boreal regions [10], and no such large landscape experiment has yet been conducted in tropical Asia. Yet this region is of critical importance, as it harbors a large fraction of the Earth's endangered biodiversity [40-41] and is where the conservation status of threatened species has deteriorated most rapidly in the last three decades [42].

In a southeast Asian context, ongoing deforestation threatens impending biodiversity losses in the region [43], a scenario that has already played out in Singapore [44]. Deforestation has been driven forward as a result of illegal logging activities that have been facilitated by corruption [45], and the logged forests become more susceptible to wild fires [46], which greatly amplify the negative effects of forest loss upon biodiversity. Moreover, the proliferation of oil palm plantations in Southeast Asia is placing tremendous pressure on forest cover [47-48]. Oil palm is the world's primary source of vegetable oil and fat [49] and one of the world's most rapidly expanding crops [48]. Developing biofuel markets are likely to further increase global demand for palm oil, which generates high yields at low costs [48] creating large profit margins [29]. Oil palm revenue already accounts for almost 2 % of the gross national income of Indonesia and more than 5 % for Malaysia [50]. These economic drivers puts tremendous pressure on the remaining, and shrinking, forests. Part of the stimulus for biofuels is a desire to reduce carbon emissions from fossil fuels, but total carbon emission reductions are unlikely to be achieved when tropical forests are cleared to make way for oil palm plantations [48, 51].

The SAFE Project will be embedded in a planned conversion of logged, lowland dipterocarp forest to oil palm plantation. Over the duration of the experiment, the matrix surrounding the forest fragments will change as the plantation progresses from a cleared forest through the process of terracing, planting of cover crops and oil palm, and the gradual maturation of oil palm which should form a canopy approximately seven years after planting. Although the matrix will change through time, at any given point in time all the fragments will be surrounded by a matrix in a similar state. This means that it will not be possible to experimentally test matrix effects in this project. Nonetheless, SAFE represents substantial advances over existing forest fragmentation experiments. Perhaps most importantly, SAFE represents the first opportunity to experimentally test the effects of landscape forest cover on ecological patterns within isolated patches. By locating the experimental blocks in positions to maximise the range of naturally-occurring forest cover in the wider landscape surrounding the experimental fragments, we allow for direct tests of the ways in which landscape forest cover may moderate patch-level effects. This has been achieved without sacrificing the ability to detect patch-level effects, and while ensuring that results from this project will be directly comparable to those of existing experimental forest fragmentation studies. Moreover, the unification of a hierarchical, fractal-based sampling scheme with the spatial layout of the fragments will allow greater integration of data collected on ecological patterns and processes that operate over very different spatial scales. The riparian component of the project will help resolve the question of how to design effective corridors so as to protect water resources and aquatic biodiversity. Finally, the use of three control habitats inserts the experimentally fragmented landscape into a wider gradient of habitat modification and land use intensity, allowing for a much broader understanding of the biotic and abiotic impacts of land use change.

The reality of a 'natural ecosystem' is fast disappearing as humans modify the world at an ever-accelerating pace, meaning much of the world's biodiversity must now perish or persist in human-modified landscapes [7]. Understanding how much of the diversity of life will persist in the future will require a better understanding of ecological processes that occur when remnants of natural habitats are embedded in a matrix dominated by human activitites [52]. The SAFE Project will be one of the world's largest ecological experiments and is designed to directly address questions about how logging, forest fragmentation and deforestation modify the functioning of tropical rainforests, impair their ability to deliver ecosystem services, and reduce their capacity to support the diversity of life.

Acknowledgements

We thank the Sime Darby Foundation, the Sabah Foundation, Benta Wawasan, and the Sabah Forestry Department for their generous support of the SAFE Project. Mick Crawley, Charles Godfray, Bill Laurance, Georgina Mace and Stuart Pimm provided valuable advice on the project design. This paper arose from a workshop sponsored by the NERC Centre for Population Biology. Researchers are invited to take advantage of the SAFE study sites and, if interested, should visit the project website (www.safeproject.net).

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Table 1: The land use intensity gradient incorporated into the SAFE Project, extending from primary forest through to oil palm plantation. Blocks correspond to the sampling sites illustrated in Fig. 2 and are ordered from least to most disturbed.

Block	Habitat	Logging	Fragmentation*	Forest cover[†]	Forest quality (range)[‡]	Notes
OG1	Forest	Never	Continuous	100 %	4.44 (3-5)	> 1 km from reserve boundary
OG2	Forest	Never	Continuous	100 %	4.88 (4-5)	> 500 m from reserve boundary
OG3	Forest	Low intensity	Continuous	100 %	4.22 (3-5)	Lightly logged 1970s and 1990s
LF1	Forest	Twice	Continuous	100 %	3.22 (3-4)	Twice logged
LF3	Forest	Twice	Continuous	76 %	3.44 (3-4)	Twice logged
LF2	Forest	Twice	Continuous	86 %	3.67 (3-4)	Twice logged
LFE	Forest	Twice	Continuous	71 %	3.25 (2-4)	Twice logged
VJR	Forest	Variable	Fragmented	61 %	3.43 (2-5)	Logged around edges, never logged in the steep interior
B	Forest	Twice	Fragmented	50 %	2.75 (2-4)	Twice logged
D	Forest	Twice	Fragmented	35 %	2.06 (1-3)	Twice logged
F	Forest	Twice	Fragmented	34 %	2.50 (1-3)	Twice logged
A	Forest	Twice	Fragmented	26 %	2.25 (1-4)	Twice logged
E	Forest	Twice	Fragmented	21 %	1.94 (1-4)	Twice logged
C	Forest	Twice	Fragmented	16 %	2.06 (1-4)	Twice logged
OP3	Oil palm	NA	Cleared	15 %	NA	Planted 2000; closed canopy; some cover crop; 1 km from forest
OP2	Oil palm	NA	Cleared	40 %	NA	Planted 2006; canopy just forming; cover crop; 500 m from forest
OP1	Oil palm	NA	Cleared	15 %	NA	Planted 2006; canopy just forming; cover crop; 700 m from forest

*Fragmentation: Continuous forest cover means the sampling block is located in a contiguous forest management area of approximately one million ha.

† Forest cover: the average amount of forest cover in a 3-km radius surrounding 2^{nd} order sampling points within each block. No distinction is made between primary and logged forest.

‡ Forest quality: average forest quality at 2^{nd} order sampling points within each block. Quality is scored on a qualitative scale of 1-5; (1) very poor, no standing trees, open canopy with ginger, vines or low scrub; (2) poor, open canopy with occasional small trees over a ginger and vine layer; (3) okay, small trees abundant and canopy at least partially closed; (4) good, lots of trees including some large trees and a closed canopy; (5) very good, no evidence of logging, closed canopy with large trees.

Table 2. Variation in the amount of forest cover surrounding experimental blocks in the SAFE Project. (*a*) Values represent the *F* and *P*-values from a mixed effect model testing for different forest cover amounts among the experimental blocks at five spatial scales. (*b*) Mean forest cover (± 1 SE) surrounding sampling points in each of the six experimental blocks. (*c*) Pearson correlation coefficient between forest cover at the five spatial scales. Values in **bold** are significant with $P < 0.05$.

Landscape	*(a)* Block		*(b)* Forest cover (%)						*(c)* Correlation			
scale	$F_{(5,18)}$	*P*	A	B	C	D	E	F	2 km	3 km	4 km	5 km
1 km	0.78	0.356	34(1)	36(3)	26(2)	36(3)	33(1)	33(2)	**0.90**	0.79	0.55	0.39
2 km	**7.15**	**0.003**	26(1)	36(2)	14(1)	33(1)	21(1)	32(2)		**0.92**	0.69	0.51
3 km	**31.31**	**<0.001**	26(1)	50(1)	16(1)	35(1)	21(0)	34(1)			**0.92**	0.80
4 km	**44.36**	**<0.001**	26(1)	57(1)	26(1)	33(1)	26(0)	32(1)				**0.97**
5 km	**59.23**	**<0.001**	26(1)	59(1)	34(1)	35(0)	30(0)	31(0)				

Table 3. The potential of six variables to confound future analyses of data emerging from the SAFE Project. Values represent the *F* and *P*-values from a mixed effect model. Significant relationships are in **bold**.

Variable	Block		Fragment area		Transect order		Area × Transect	
	$F_{(5,18)}$	P	$F_{(3,15)}$	P	$F_{(3,60)}$	P	$F_{(9,60)}$	P
Longitude	**502.279**	**<0.001**	1.102	0.944	0.007	0.998	1.657	0.447
Latitude	**75.906**	**<0.001**	0.155	0.998	0.060	0.932	0.205	0.999
Altitude	1.136	0.233	1.432	0.796	0.137	0.514	0.686	0.859
Slope	0.123	0.930	0.820	0.753	0.713	0.570	0.287	0.982
Pre-fragmentation land use	**19.377**	**<0.001**	1.708	0.927	0.020	0.345	1.806	0.303
Isolation	**24.530**	**<0.001**	0.906	0.991	0.548	0.861	1.340	0.558

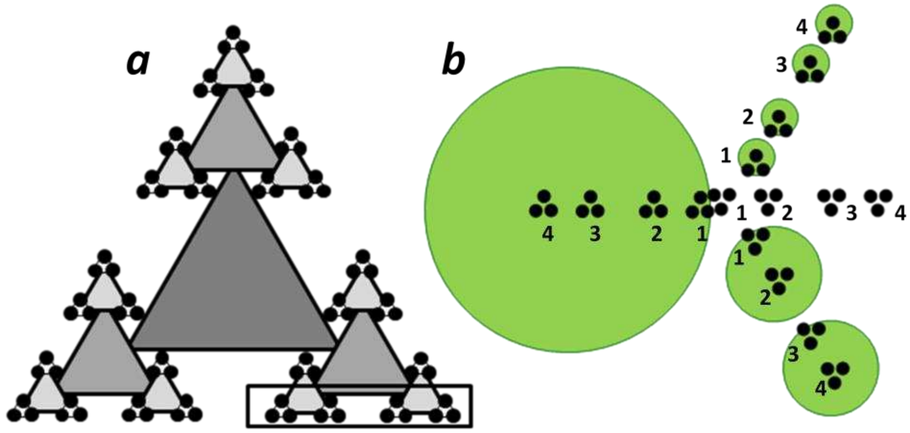
Figure captions

Figure 1. (a) Fractal geometry of the sampling network in a continuous habitat. Points on the vertices of the white triangles represent sampling locations, and triangles of progressively darker shades indicate a progression from the first to fourth order of the fractal pattern respectively. The box on the lower right encompasses a sampling transect that is used as the basis of the sampling scheme in the forest fragments. (b) Spatial layout of fragments forming a single block in the split-plot experimental design of the SAFE Project, showing how the fractal sampling scheme is embedded within each fragment (circles) and the surrounding matrix. The experimental block is formed of four plots: (1) 1 × 100-ha fragment; (2) 2 × 10-ha fragments; (3) 4 × 1-ha fragments; and (4) samples in the matrix adjacent to the 100-ha fragment. Total sampling effort, and the spatial distribution of sampling effort, is exactly the same within all plots. Numbers 1-4 represent the 'transect order' of sampling points within plot, which is used in analyses of the potential impact of confounding variables.

Figure 2. Map of the Stability of Altered Forest Ecosystems Project, located in Malaysian Borneo. The project encompasses a gradient of forest modification encompassing (a) old growth and lightly logged forest; (b) continuous, twice-logged forest; (c) twice-logged and fragmented forest in an oil palm matrix; and (d) continuous oil palm plantation. (e) The fragmentation experiment comprises six blocks (A-F), each with seven fragments arranged as shown in Fig. 1. In addition to the experimental fragments themselves, sampling across edge gradients will occur in a Virgin Jungle Reserve (VJR) adjacent to the experimental area and at the edge of continuous logged forest (LFE) to the north of

the experimental area. Fragments are currently embedded in a twice-logged forest landscape that will be converted to oil palm as part of the experiment (labeled ‘Oil palm (future)’). The riparian corridor experiment comprises six watersheds located within the experimental area. Sampling points show the locations of the 2nd order fractals across the study area. The OG3 block of control sites in Maliau Basin falls within the water catchment of the Maliau Basin Field Centre and has been selectively logged.

FIGURE 1



755 **FIGURE 2**

756