Tropical Forest Fragmentation; Implications for Ecosystem Function.

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Greenpeace Research Laboratories Technical Report (Review) 02-2014: 15pp.

Executive Summary

Tropical forests are home to more species than nearly any other ecosystem on the planet but this biodiversity is becoming increasingly threatened. When forest is cleared, this obviously results in a reduction in forest area. However, there is also another, less obvious but highly damaging impact, whereby the remaining areas of forest become broken up into isolated patches or fragments. This fragmentation directly harms many species and alters the environmental conditions within the forest. It also disrupts multiple important interactions between species. To give just one example, pollination may be reduced if pollinator species cannot move between isolated forest fragments. As ecosystems are composed of the interacting species present and the physical environment they inhabit, fragmentation therefore has a clear potential to alter how the entire forest ecosystem functions.

Ecosystem function is difficult to study due to its complexity and the long time-scales involved. However, there is now a growing body of evidence relating ecosystem function to tropical forests fragmentation. In drawing together these findings, this review highlights a number of key impacts. These include dramatic increases in herbivore numbers due to the loss of top predators, ever-increasing vulnerability of fragmented forest to fire and the disruption of seed dispersal mutualisms which are crucial to the persistence of many tropical tree species. Such changes may reduce the resistance, resilience and overall stability of tropical forest ecosystems. This review highlights the importance of preserving large areas (500 km^2+) of intact forest in order to prevent fragmentation from altering ecosystem function, as such changes are likely to be both very harmful and extremely difficult to reverse.

In this review, the impacts of fragmentation that may have consequences for ecosystem function are described under two sections; abiotic impacts (Section 2.0) and ecological impacts (Section 3.0). Abiotic impacts include any changes to non-living elements of the ecosystem, such as physical changes to the microclimate, while ecological impacts covers changes to species interactions. The overall likely consequences for ecosystem function of these changes are then summarised in the final section (Section 4.0).

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Summary of Abiotic Impacts

Fragmentation strongly alters the microclimate near to forest edges, leading to edges becoming much drier, and also strongly increasing wind speeds. This can cause the death of many large trees characteristic of primary, undisturbed forest. The species which replace them tend to be less woody, significantly lowering the amount of carbon the forest can store. Fragmentation also alters the local water cycle, with stream becoming more prone to either floods or droughts. Finally, the vulnerability of forests to fire is strongly affected. Normally, rainforest is very fire resistant. However, the drier conditions and increased amount of dead wood (i.e. fuel for fires) in edges and fragments makes them very fire prone. This can lead to a worsening cycle of vulnerability, with each successive fire making the next more likely.

Summary of Ecological Impacts

Pollination: Most tropical trees rely on animals for pollination. Long distance pollination is necessary to connect populations isolated in forest fragments, but is generally only possible by large species, like birds and bats. Many insect pollinators, such as Eugulossine (or orchid) bees, will not even cross gaps as narrow as 100 m. Unsurprisingly, current evidence suggests fragmentation to have a large and negative impact on pollination and hence plant reproduction.

Seed dispersal: In some tropical regions, up to 90% of tree species are dispersed by animals. Many studies show fragmentation to be disrupting this vital process. Certain groups of species are more strongly impacted, particularly specialist species and large-seeded trees. Large-seeded trees are particularly vulnerable because fragmentation often causes the loss of nearly all large-bodied animals capable of dispersing large seeds. For instance, a study in Mexico found fragments <30 ha had virtually no large-bodied seed dispersers, causing the survival of seeds from large-seeded trees to drop by ~50%.

Herbivory and Predation: There is a growing recognition of the important role played by predators in regulating ecosystems. Large predators are very susceptible to fragmentation, meaning they are often absent from fragmented forest. The loss of top predators can trigger trophic (food-web) cascades, where populations of species lower down the food chain multiply out of control. This has been seen from herbivores such as wild pigs, leaf-cutter ants, howler monkeys and rodents, with densities becoming 10-100 times higher than in intact forest. A review carried out in 2012 concluded that fragmentation-induced trophic cascades are now having catastrophic impacts on tropical forests worldwide, showing the presence of top predators to be a fundamental component of a functionally health tropical forest ecosystem.

Likely Overall Impacts to Ecosystem Function

Evidence of the abiotic (Section 2.0)and ecological impacts (Section 3.0) of fragmentation indicate that fragmentation strongly alters multiple aspects of ecosystem function. This is likely to significantly reduce the stability and resilience of tropical forest ecosystems, especially given the high proportion of species dependent on mutualistic interactions which are easily disrupted by fragmentation, such as pollination and seed dispersal.

Furthermore, forest fragmentation has been shown to significantly reduce biodiversity. Whether higher biodiversity leads to more robust ecosystem functioning has long been debated however recent research is increasingly showing this to be the case, providing further evidence that fragmentation must be avoided to preserve healthy ecosystem function.

Finally, fragmentation is not the only threat facing tropical forests. Tropical forests are also at high risk from climate change, invasive species and over-hunting. Worryingly, fragmentation increases the vulnerability of tropical forests to these other threats. For instance, it makes previously remote areas of forest easily accessible to hunters, blocks species from moving as the climate changes, reduces the residence of forest communities to invasive species *etc*. This means there is a risk to allowing any level of fragmentation of tropical forests, as once the process has begun, it may be difficult to prevent it from continuing. Therefore a precautionary approach is required in which large, intact areas of primary forests are protected from fragmentation.

1.0 Introduction

Defined as an unbroken expanse of primary forest greater than 500 km^2 without significant human activity, intact forest landscapes comprise only 29.9% of the world's remaining tropical forests (Gibson et al., 2011; Potapov et al., 2008). This surviving fraction is rapidly being broken up and fragmented (Wright, 2005). This raises the urgent question of how fragmentation will impact on ecosystem function, the essential set of processes which maintain tropical forest ecosystems (Laurance et al., 2011). Research has now been carried out into several aspects of how forest fragmentation impacts ecosystem function. This review brings together this research, in order to elucidate the full implications of tropical forest fragmentation.

Forest fragmentation is the breaking up of contiguous forest into blocks (Davidson, 1998). Ecosystem function can be defined as the processes that collectively contribute to the self-maintenance of an ecosystem. Ecosystem function can be divided into biogeochemical and ecological processes (Naeem et al., 2012). Together, these processes shape and sustain the overall functioning of an ecosystem, including its stability, resistance and resilience (Cardinale et al., 2006; Naeem et al., 2012; Richmond et al., 2005).

Fragmentation creates forest fragments surrounded by 'matrix' habitat, which varies from secondary forest to intensive agricultural land (Lewis, 2009). Isolation, small population sizes and edge effects, amongst other factors, have deleterious impacts within these fragments (Turner, 1996). Many species, especially specialists and those requiring large ranges, thus eventually become extinct in fragmented forest (Turner, 1996). This lag time between extinctions and their underlying cause is referred to as extinction debt and may continue for decades or more following fragmentation (Honnay et al., 2005; Pütz et al., 2011; Vranckx et al., 2012).

This review begins by outlining the effects of the abiotic impacts of fragmentation to biogeochemical and physical processes, including biomass, carbon storage, fire regime and hydrology. Impacts to the ecological processes of pollination, seed dispersal, herbivory and predation are then described in more detail. Finally, the combined implications of these impacts to ecosystem function are discussed.

Although the aspects of ecosystem functioning covered here are the best understood and most studied, current understanding is still incomplete (Laurance, 2005; Robinson & Sherry, 2012). This review, therefore, presents a synthesis of fragmentation impacts to ecosystem function according to available scientific knowledge, whilst also highlighting gaps in current understanding.

2.0 Abiotic Impacts of Fragmentation

The abiotic impacts of fragmentation can cause significant changes to the physical environment within forests and to biogeochemical processes (Laurance et al., 2011). The most important and pervasive of these effects are summarised here. A more detailed review of the abiotic impacts of fragmentation is available as a Greenpeace Technical Note (Thies et al. 2011).

Key abiotic conditions and processes affected include forest microclimate, biomass and carbon storage, fire regimes and hydrology (Cochrane & Laurance, 2002; Laurance et al., 2011; Numata et al., 2011). Closed-canopy tropical forests are characterized by a highly stable, humid, dark microclimate, to which many species are specifically adapted (Laurance et al., 2009). Edge effects are an important aspect of fragmentation. They can be defined as diverse environmental changes associated with the abrupt, artificial boundaries of forest fragments and they strongly alter the normally stable forest microclimate (Laurance et al., 2006). Most edge effects penetrate up to 100-300 m from forest edges, though distances of 1 km are not uncommon (Gascon et al., 2000). The strength of edge effects depends on edge age and structure, the surrounding matrix and proximity to other edges (Didham & Lawton, 1999; Laurance et al., 2011). Edge effects lower humidity and increase light, temperature, wind disturbance and desiccation (Laurance et al., 2011). These physical alterations lead to sharply increased tree mortality in edges (Laurance & Ferreira,1998.; Laurance, 2004; Laurance et al., 2006). Large trees (>60 cm diameter) are particularly vulnerable; in central Amazonia these trees were found to die 281% faster in edges (Laurance et al., 2000). Pioneer species, in contrast, are suited to these conditions, leading to a shift in species composition toward earlier successional states; a process known as retrogressive succession (Laurance & Ferreira, 1998; Pütz et al., 2011; Santos et al., 2008). Pioneer species are smaller and have lower wood density, hence fragmented forests have markedly lower biomass and hence sequesters much less carbon (Laurance et al., 2011; Laurance, 2004; Numata et al., 2011; Pütz et al., 2011). Worldwide, this fragmentation-induced died back of large trees and their subsequent replacement with early succession species releases 150 million tonnes of carbon annually, higher than the UK's current annual carbon emissions (Laurance et al., 2011; Numata et al., 2011).

Hydrological regimes of fragmented forests also differ markedly from intact forests (Laurance et al., 2011). Fragmentation reduces evapotranspiration and infiltration and increases stream flow variation, resulting in increased incidences of flooding and stream failure (Giambelluca, 2002; Laurance et al., 2011; Rodriguez et al., 2010). Another, large scale, effect triggered by fragmentation is the 'vegetation breeze'. This effect causes clearings to draw moist air away from forests, resulting in less rain falling over forests and further exacerbating desiccation in fragments (Laurance et al., 2002; Laurance et al., 2011).

Closed-canopy rainforests are usually highly resistant to fire due to their humid microclimate and the rapid decomposition of leaf litter (Laurance, 2004). Increased desiccation means fragments, in contrast, have dry, fire-prone edges; distance from forest edges explains up to 92% of observed burning in the Amazon (Cochrane & Laurance, 2008; Laurance et al., 2002). Closed-canopy rainforest vegetation is not adapted to deal with fire, so even fires of low intensity kill around 40% of trees and nearly all vines (Cochrane & Laurance, 2002; Gascon et al., 2000; Laurance, 2004).

Damaged vegetation continues to die slowly for up to 2 years, after a fire. This build-up of fuel, along with increased desiccation due to further opening of the canopy, creates a positive feedback where each subsequent fire increases the likelihood and severity of the next (Cochrane et al., 1999). This can lead to receding forest edges as fragments 'implode' inwards (Gascon et al., 2000). A very concerning concept given that over 13% of the Amazon is already vulnerable to edge-related fires (Cochrane & Laurance, 2002; Cochrane, 2001).

In summary, altered abiotic conditions resulting from fragmentation cause hydrological regimes to become much more dynamic. They also sharply increase tree mortality in edge habitat, markedly lowering biomass and reducing carbon storage. These changes strongly alter the fire regime in fragmented forest and have the potential to trigger a positive feedback of ever-increasing vulnerability to fire in edge habitat.

3.0 Fragmentation Impacts on Ecological Processes

This section presents a synthesis of known fragmentation impacts to four of the most fundamental ecological processes shaping ecosystem function, pollination, seed dispersal, herbivory and predation.

3.1 Pollination

As pollination directly affects plant reproduction, impacts of fragmentation on pollinators could have wide-reaching consequences for tropical forest plants (Didham et al., 1996). Most tropical trees rely on animals for pollination, depending on these mutualisms to maintain genetic diversity and prevent inbreeding (Laurance, 2005).

Fragmentation has been shown to reduce the abundance and diversity of pollinators and, though less well understood, may also alter pollinator behaviour and movement patterns (Didham et al., 1996). A key study of impacts on pollination in forest fragments in Argentina found median decreases in pollination levels and seed output in fragments approached 20% (Aizen & Feinsinger, 1994). In 2006, a meta-analysis of plant reproductive susceptibility to fragmentation found a large negative effect on both pollination and plant reproduction (Aguilar et al., 2006). Plant compatibility system, which ranges from self-compatible to self-incompatible, was the only reproductive trait which explained the different effect size between species, with self-incompatible plants more dependent on pollinators, and hence more vulnerable to fragmentation.

Pre-2004, it was assumed that pollinator-specialist plants, which interact with only one or a few pollinators, would be more vulnerable to fragmentation than generalist plants (Ashworth et al., 2004). However, it has since been found that specialist plants tend to be pollinated by generalist pollinator species and generalist plants by more specialised pollinators (Ashworth et al., 2004; Vázquez & Aizen, 2004). These asymmetric interactions mean specialist plants are no more vulnerable than generalists, making pollination networks more robust to fragmentation in this regard (Ashworth et al., 2004; Hadley & Betts, 2012).

The response of pollinators themselves to fragmentation can vary considerably, though insect pollinators appear to be most sensitive (Aizen et al., 2002; Kearns et al., 1998). Long distance pollination, required if genetic diversity is to be maintained across fragments, is only likely to be possible for larger pollinators like birds and bats (Laurance, 2005; Vranckx et al., 2012). One bat species, for instance, has been found to regularly fly 1 km or more between fragments (Law & Lean, 1999). However, a large proportion of tropical forest species will not cross even narrow clearings (Laurance et al., 2009). For example, Euglossine (or orchid) bees, pollinators of many neotropical orchids, will not cross 100 m wide open spaces (Powell & Powell, 1987).

Wind-pollinated plants may also be vulnerable to reduced pollination (Ghazoul, 2005). The efficiency of wind pollination drops sharply as the distance from a pollen source increases, leaving spatially isolated populations of wind-pollinated trees vulnerable to pollen limitation (Vranckx et al., 2012).

The full impact of fragmentation on pollination and plant reproduction are not yet fully understood (Hadley & Betts, 2012) but current evidence indicates that the impacts can be substantial. Some scientists have even suggested it could constitute the first step towards the demographic collapse of many plant populations (Aizen et al., 2002).

3.2 Seed Dispersal

Seed dispersal is fundamental to the structuring and functioning of rainforest communities (Dennis & Westcott, 2006). In tropical regions, the seeds of up to 90% of plant species are dispersed by animals (Farwig & Berens, 2012). For these species, seed dispersal provides a way to to collonise new areas and avoid the high levels of competition and natural enemies found near parent plants (Howe & Smallwood, 1982).

A number of studies have found detrimental impacts of fragmentation on seed dispersal; in fragmented landscapes plant recruitment may often be dispersal-limited (Cordeiro & Howe, 2003; Cramer et al., 2007; Herrera & García, 2010; McConkey et al., 2012). In forest fragments in Tanzania, recruitment of 31 animal-dispersed tree species was 4 times lower in small fragments than contiguous forest and 40 times lower for the 10 endemic species studied (Cordeiro and Howe, 2001).

Specialist plant species, i.e. those depending on a specific disperser species, are highly vulnerable (Farwig & Berens, 2012). Fortunately, the majority of seed dispersal relationships are generalist and non-obligate (Dennis & Westcott, 2006; Menke et al., 2012), though it should be noted that overall understanding of redundancy in dispersal networks remains poor (McConkey et al., 2012).

A key concern is the vulnerability of large-seeded trees due to the loss of large frugivores (Cordeiro & Howe, 2001; Wotton & Kelly, 2011). In southern Mexico, fragments <30 ha have virtually no large frugivores and recruitment of large-seeded species is these fragments in <25%, half that found in fragments >640 ha (Melo et al., 2010). In Brazil’s Atlantic forest, forest fragments contain <35% of the large-seeded trees found in contiguous forest (Santos et al., 2008). Large-bodied frugivores capable of dispersing large seeds are more likely to be impacted by fragmentation as they require larger areas of contiguous forest (Turner, 1996). Also, they are often subject to hunting, which interacts synergistically with fragmentation (discussed in detail in section 4.0.) (Farwig & Berens, 2012; Peres, 2002).

A recent study on a keystone species (one that plays a critical role in maintaining the structure of an ecological community) of palm in Brazil’s Atlantic forest found evidence of rapid evolutionary change in seed size due to the functional extinction of large frugivores after fragmentation (Galetti et al. 2013). This lack of large avian frugivores in fragmented forest has resulted in a significant reduction in seed size over several decades, as the tree species was selected to produce seeds that can be dispersed by the remaining smaller avian fauna. This is particularly concerning as these smaller seeds show reduced probability of recruitment; being less likely to germinate, more prone desiccation and more quickly attacked by fungi. The study suggests such findings are likely to be applicable to many large-seeded tropical tree species, demonstrating the potential for the functionally extinction of large frugivores in forest fragments to substantially impact ecosystem function.

While the importance of each frugivore species varies, some individual species can have a strong community-wide effect. For instance, Congo forest elephants (*Loxodonta africana cyclotis*) are keystone long-distance seed dispersers; evidence suggests they consume more seeds from more types of species than any other taxon of large vertebrate and could be essential for ecosystem function in the region (Campos-Arceiz & Blake, 2011). They are also very sensitive to fragmentation, with roadless wilderness area being a strong determinant of their home range size (Blake et al., 2008). Through restricting forest elephant movements, fragmentation could substantially alter tree species composition across the Congo Basin (Campos-Arceiz & Blake, 2011).

Overall, the impacts of fragmentation on seed dispersal are likely to reduce the abundance of primary-forest trees, especially endemics, seed-disperser specialists and large-seeded trees (Costa et al., 2012; Farwig & Berens, 2012; Kirika et al., 2008), further re-enforcing the process of retrogressive succession (Santos et al., 2008). The functional extinction of large frugivores, in particular, could be highly detrimental and appears likely to result in rapid evolutionary changes (da Silva & Tabarelli, 2000; Galetti et al. 2013; Terborgh et al., 2008).

3.3 Herbivory

Plant-herbivore interactions are important in shaping ecosystem functioning and can strongly influence the structure and dynamics of forest communities (Ruiz-Guerra et al., 2010; Wirth et al., 2008). Herbivore populations are influenced chiefly by a combination of bottom-up forces (resource availability) and top-down forces (predator pressure) (Richards & Coley, 2007).

Excluding fragmentation-induced changes to top down regulation (described in detail in Section 3.4 Predation), the evidence for fragmentation impacts to herbivory is mixed, with both population increases and decreases having been recorded (Ruiz-Guerra et al., 2010; Wirth et al., 2008). Herbivory rates may decrease in isolated fragments (Ruiz-Guerra et al., 2010), potentially because of reduced populations of herbivorous insects (Laurance et al., 2011). Harsher abiotic conditions and lack of food plants in matrix habitat may present a dispersal barrier for many insects, limiting immigration into isolated fragments (Fáveri et al., 2008). As insects can account for around 70% of herbivory in some tropical forests (Coley & Barone, 1996), this could result in a significant change in herbivory rates.

In contrast, herbivory appears to increase in edge habitat (Laurance, 2005; Wirth et al., 2008). Many herbivores, especially generalists (Wirth et al., 2008), appear to benefit profoundly from forest edges. The shift in tree species composition in edges results in a greater prevalence of pioneer species which tend to be more palatable to herbivores. Many pioneer plant species have both fewer defences against herbivory and higher nutritional content (Farji-Brener, 2001; Urbas et al., 2007). This can therefore result in a relaxation in bottom-up control on herbivory in edges as food availability is increased.

One of the best studied examples of this is the effect of fragmentation on the leafcutter ant (LCA) (Michel & Sherry, 2012). LCAs are dominant herbivores and ecosystem engineers in neotropical forest and become hyper-abundant in forest edges (Meyer et al., 2006; Meyer et al., 2009; Wirth et al., 2007). This is due to multiple factors, the most significant of which is the increase in pioneer plant species (Urbas et al., 2007). A literature review found pioneer species were harvested 3 times more frequently than shade-tolerant species, making up the majority of the LCA's diet in all studies reviewed (Farji-Brener, 2001). Also, increased desiccation due to fragmentation benefits LCAs; they prefer to harvest drought-stress leaves as these also have an increased nutritional value (Meyer et al., 2006). Intense herbivory pressure from LCAs further increases light penetration into edges, amplifying already damaging edge effects by further increasing variation in temperature and humidity (Urbas et al., 2007) and potentially speeding the shift toward increased prevalence of pioneer species. However, other effects of fragmentation are also involved in LCA hyper-abundance, such as the lack of predation from armadillos in fragments (Rao, 2000) and reduced abundance of natural enemies such as parasitic phorid flies (de Almeida et al., 2008).

Current knowledge suggests the potential for important changes in herbivory rates (Wirth et al., 2008), particularly regarding herbivorous insects (Fáveri et al., 2008; Laurance, 2005) and, in the neotropics, effects of fragmentation on LCAs (Meyer et al., 2009; Wirth et al., 2007). Further research is urgently needed on how the contrasting findings of decreased herbivory in isolated fragments but increased herbivory in edges plays out, given that small fragments are often composed almost entirely of edge-effected habitat.

3.4 Predation

There is growing recognition of the important role played by predators in regulating ecosystems and sustaining biodiversity (Ritchie & Johnson, 2009). There is even evidence to suggest that a small loss of diversity from the highest trophic levels can a have an impact on ecosystem function equivalent to a large reduction of diversity at lower trophic levels (Duffy, 2003).

Large predators are very susceptible to fragmentation impacts as they require large home ranges, are highly edge-sensitive, have vulnerable life-history traits and are often subject to hunting (Duffy, 2003; Michel & Sherry, 2012). One potential consequence of the loss of apex predators due to fragmentation is the triggering of a trophic cascade as herbivore populations are released from top-down control. Such trophic cascades are considered by some to be as serious a threat to tropical biodiversity as climate change (Michel & Sherry, 2012).

One of the best documented cases of this comes from Venezuela. In 1986, a large number of islands of varying sizes were created by the formation of Lago Guri reservoir, providing an opportunity for scientists to track the resulting changes to the newly isolated fragments (Terborgh et al., 2006). Small and medium-sized islands were too small for predators of vertebrates to survive. In their absence, densities of herbivores; rodents, howler monkeys, iguanas, and leaf-cutter ants, became 10-100 times greater than in mainland unfragmented forest (Terborgh et al., 2001). This herbivore hyper-abundance has transformed the island plant communities. By 2002, tree sapling density on small islands had fallen to 25% of that on the mainland, due largely to leaf cutter ant herbivory (Rao, 2000; Terborgh et al., 2006). Mortality of woody plants on herbivore-impacted islands now exceeds recruitment in nearly all species. Some small islands have now reached the 'post leaf-cutter ant' phase, where the forest canopy has died without replacement and the remaining vegetation is entirely dominated by herbivore-resistant lianas (Terborgh et al., 2006).

It is not certain to what extent this example applies to 'real' forest fragments, which are not islands but are surrounded by a matrix of modified land and, also, are generally subject to hunting (Laurance, 2005). Hunting and fragmentation are tightly linked and it is possible that trophic cascades may often be prevented from occurring because humans replace natural apex predators and maintain top-down control (Turner, 1996; Wright et al., 1994).

There are now a number of other studies documenting trophic cascades in more natural tropical forest systems. A review carried out in 2012 concluded that fragmentation-induced trophic cascades are now having catastrophic impacts on tropical forests worldwide (Michel & Sherry, 2012). To give an example, lack of predator pressure has contributed to hyper-abundance of native wild pigs in Pasoh Forest Reserve, Malaysia. The wild pigs have reached a density 10-100 times greater than that observed in forests with predators present (Ickes, 2001). Pig nest-building activities are a major source of tree sapling mortality and substantial shifts in tree community composition are expected (Ickes et al., 2005).

Another potential consequence of the loss of apex predators is the disproportionate (up to fourfold) increase in abundance of middle-ranked predators (Prugh et al., 2009; Ritchie & Johnson, 2009). This is termed mesopredator release and can have major impacts on nesting bird populations (Sieving, 1992), and also on large-seeded tree species, as seed predators abundance increases (Laurance, 2009). As yet, there does not appear to be any research on the relationship between mesopredator release and trophic cascades due to herbivore hyper-abundance. Therefore, which circumstances are likely to predispose a system toward one or other of these opposing responses remains unclear.

In either case, a viable carnivore guild appears to constitute a fundamental part of the maintenance of biodiversity and ecosystem processes, making large extents of intact forests an essential conservation requirement (Michel & Sherry, 2012; Terborgh et al., 2006).

4.0 Summary: Implications of Forest Fragmentation for Ecosystem Function

Tropical forests, the most biodiverse terrestrial ecosystem on the planet (Lewis, 2009), are subject to one of the highest rates of habitat fragmentation of any biome (Laurance, 2004; Lewis, 2009). Evidence of the physical and ecological impacts of fragmentation described above indicates that fragmentation substantially alters ecosystem function.

Impacts to biogeochemical processes include more variable hydrological regimes and markedly reduced biomass and carbon storage capacity (Giambelluca, 2002; Laurance et al., 2011). Fire regimes are also dramatically affected, as the altered microclimate in edges triggers a positive feedback leading to ever-increasing frequency and intensity of fires with the potential to cause fragments to ‘implode’ inwards (Cochrane & Laurance, 2002; Cochrane et al., 1999; Gascon et al., 2000).

Fragmentation-induced changes to ecological processes have numerous impacts on ecosystem function (Valladares et al., 2012). Loss of apex predators can trigger trophic cascades which dramatically alter plant communities through releasing herbivores from top-down control (Ickes, 2001; Ickes et al., 2005; Michel & Sherry, 2012; Terborgh et al., 2001; Terborgh et al., 2006). Disruption of seed dispersal and pollination causes strong detrimental impacts to rainforest tree communities (da Silva & Tabarelli, 2000; Lopes et al., 2009). Many tree species that are obligate outbreeders decline (Lopes et al., 2009) and gene flow between fragmented populations can be impeded (Aguilar et al., 2008; Bijlsma & Loeschcke, 2012). Animal-dispersal dependent tree species also suffer (Farwig & Berens, 2012; Kirika et al., 2008; Lamb et al., 2005; Laurance et al., 2006; Menke et al., 2012; Sekercioglu, 2006); particularly large-seeded tree species, more than two-thirds of which can be lost from highly fragmented landscapes (Santos et al., 2008). Co-dependency is inherent in mutualistic interactions. Hence, declines within these tree genera cause further declines to the animal species performing seed dispersal and pollination processes, due to loss of fruit and flower resources (Laurance et al., 2006), potentially creating a self-reinforcing cycle (Laurance et al., 2006; Tabarelli et al., 1999). Such declines are likely to cause significant reductions in genetic diversity (Aguilar et al., 2008; Bijlsma & Loeschcke, 2012; Honnay et al., 2005) and result in an impoverished functional community of tree species (Lopes et al., 2009).

Fragmentation impacts on ecosystem function are likely to reduce ecosystem stability through reducing resistance and resilience. Resilience describes the speed with which a system returns to its former state after displacement, while resistance is its ability to avoid displacement to begin with (Begon et al., 2005). Reduced seed dispersal, particularly of large-seeded trees, impacts forest regeneration (Costa et al., 2012; Lamb et al., 2005; Galetti et al., 2013), thereby reducing resilience. Genetic erosion, due to disruption of pollination networks, reduces resistance by reducing the ability of populations to adapt to stressors (Bijlsma & Loeschcke, 2012). Loss of apex predators appears to substantially reduce ecosystem stability (Michel &. Sherry, 2012), while fragmentation dramatically reduces rainforest resistance to fire (Cochrane & Laurance, 2002; Laurance, 2004). Also, many processes in fragmented forests become hyperdynamic, including disturbance regimes, hydrology and the pace of biogeochemical cycling (Laurance, 2009; Laurance et al., 2011). In addition, reduced biodiversity is likely to reduce functional stability, as this depends on the complementarity of species' responses to perturbations (Morris, 2010; Naeem et al., 2012).

These detrimental impacts on ecosystem function are exacerbated by synergisms between fragmentation and other anthropogenic threats (Williamson, 2001). Aside from fragmentation, the main drivers of tropical biodiversity loss are deforestation, over-exploitation, invasive species and climate change (Morris, 2010). Fragmentation interacts synergistically with all of these. Fragmentation increases the area of forest accessible to people, facilitating further deforestation and meaning hunting is often ubiquitous in fragmented forests (Laurance et al., 2009; Peres, 2002; Wright, 2005). Synergisms with over-exploitation are worsened because the sizes of fragments are generally below the minimum area required to support sustainable hunting in most target species (Michel & Sherry, 2012; Peres, 2002). Disturbed communities in fragments are less resistant to invasion, while altered microclimates make invasion more likely (Turner, 1996). In terms of climate change, even modest warming will increase forest vulnerability to fire (Laurance, 2004), plus fragments are much more sensitive to increased wind disturbance from extreme weather events (Laurance et al., 2011). Fragmentation is also likely to block species from shifting their distributions as the climate changes (Feeley & Rehm, 2012).

Primary, and therefore by extention, intact forests are considered to be irreplaceable for sustaining tropical biodiversity (Gibson et al., 2011). The relationship between biodiversity and ecosystem functioning has long been debated, however the latest research suggests that a strong positive relationship exists (Naeem et al., 2012). Biodiversity is often viewed simply in taxonomic terms, measured as species richness and evenness, however biodiversity also includes functional, phylogenetic, genetic, spatial, temporal, landscape, and interaction diversity (Costanza et al., 2007; Naeem et al., 2012). Conventional measures of species richness or taxanomic diversity alone frequently fail to show ecologically significant changes to communities which can have important consequences for ecosystem function (Laurance et al., 2006; Lewis, 2009). As research has moved to incorporate this more complex view of biodiversity, the linkage between biodiversity and ecosystem function has become increasingly evident (Naeem et al., 2012). This provides further support for the need to prevent fragmentation of intact forest.

Ecosystem services are the benefits humanity derives, directly or indirectly, from ecosystem function (Costanza et al., 2007). Hence, fragmentation-induced changes in ecosystem function could have important consequences for humanity (Naeem et al., 1999). While the exact relationships are uncertain, it has been suggested that a 1% loss of biodiversity (as measured by the proxy of species richness) could correspond to approximately a 1-2% reduction in the value of ecosystem services (Costanza et al., 2007).

Although our understanding of tropical forest ecosystem function remains incomplete, there is undoubtedly a strong argument for the need to preserve large areas (500 km^2+) of intact forest (Gibson et al., 2011; Laurance et al., 2011; Lopes et al., 2009; Michel & Sherry, 2012; Peres, 2002; Potapov et al., 2008; Turner, 1996). This is especially true given that it is unknown whether the transition between the ecosystem function and ecosystem services of primary forest and that of secondary forest is linear (Morris, 2010). It is possible that a tipping point could be reached above a critical threshold of fragmentation. High levels of co-dependence in tropical forests have the potential to give rise to positive feedbacks, accelerating the breakdown of functionally important mutualistic interactions. Furthermore, fragmented forest, particularly in light of retrogressive succession, is unlikely to support key functional groups involved in the maintenance of ecosystem stability, such as large frugivores and apex predators.

While it has been demonstrated that some aspects of ecosystem function can be maintained in moderately disturbed forests (Schleuning et al., 2011), the evidence presented here strongly caution against any encroachment into intact forests. In keeping with the precautionary principle, fragmentation of intact forest should therefore be prevented whenever possible, especially in light of the synergisms between fragmentation and other anthropogenic threats to tropical forests (Laurance et al., 2009). If measures are not taken to tackle the accelerating fragmentation of tropical forests then the resulting changes to the ecosystem function are likely to be highly detrimental, as well as difficult, if not impossible, to reverse (Hooper & Vitousek, 1997).

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