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## Forest Gap; A Blessing in Disguise? A Review on Gap Dynamics, Human Interpolations and Interventions

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### ABSTRACT

*This review paper aims to highlight the variances between forest gap characteristics and gap-phase regeneration in natural and anthropogenic-induced forest gaps. It also evaluates whether or not deforestation on natural tropical forest provides an opportunity for generating viable flora compositions that would have better adaptability to the continually changing environment. By comparing the differences and a range of other aspects of the two disturbance regimes, it is evident that anthropogenic disturbances may also pose an opportunity for good results in the gap-phase regeneration process, provided the extent and severity of induced disturbances mimic natural gap systems in terms of damages initiated and size. Numerous literature have been able to differentiate and to some extent quantify the above terms and associate them discretely with the two disturbance regimes, but also considering that there is some overlaps in characteristics between the two. It has been concluded in this review that natural gaps stand a better chance of recovering than anthropogenically induced gaps. However, the latter can do equally well if assisted by human ingenuity, but this is yet to be the case in a global sense.*

**Keywords:** Forest gaps, Gap dynamics, Anthropogenic disturbances, Human Interpolations and Interventions

Forest gaps and their impact on forest ecosystems have been widely studied since the early 1970s (Yamamoto 2000), as they play a driving role in the spatial and temporal changes in the forest structure and dynamic processes (Whitmore 1975; Halle *et al.* 1978). This subsequently alters the uniformity of forest communities and hence determines the composition of the forest for few decades and sometimes centuries (Whitmore 1991). This phenomenon is termed 'Gap Dynamics' and varies throughout different forest types as a function of; climate-type, biodiversity and disturbance factors (Brokaw 1985; Yamamoto 2000; Denslow *et al.* 2001). Furthermore the great deal of interest in gap dynamics over the years, was associated with the ability to forecast practical forest applications such as forest conservation practice, natural regeneration method and as well as basic ecological theories including niche partitioning, species adaptation and latitudinal gradient of species diversity (Yamamoto 2000). Yet another aspect of interest in gap dynamics succeeded as the amount of anthropogenic disturbance on natural forest accelerated exponentially over the later part of the 1900s to present times.

Gaps associated with anthropogenic activities have surely created a whole new dimension on the understanding of forest regeneration. Various studies have shown that a significant amount of biodiversity is lost in anthropogenic gaps (e.g. Denslow *et al.* 2001; Schnitzer & Carson 2001; Lamb *et al.* 2005). This conclusion was made possible through comparing species richness between the initial pristine biodiversity and regenerating gap diversity. However, it is still poorly understood on whether general fitness of pioneer species and the forest re-growth are equally compatible, or rather favours either of the two.



## Forest Gaps

Due to the exceptionally high flora diversity in tropical forest stands (Gentry 1990), the complexities in describing the levels of forest structure in gap regeneration may be equally intricate. Swaine and Whitmore (1988) proposed a discrete division of tree species into two groups or guilds, pioneer (non-climax) and non-pioneer (or climax), based on seed germination and seedling establishment. These definitions have been widely used in much recent literatures (e.g. Brown 1993; Brokaw & Busing 2000; Dietze & Clark 2008). Pioneer species are shade intolerant plants that do best in lighted conditions (Whitmore 1989). Their seeds are dispersed around the forest floor by animal vectors, water and wind movement (Keane & Finney 2006). The seeds lie dormant on the forest floor until enough light is available to germinate. Seeds of some species survive in dormancy for very long periods of time (Lamb 1998).

Non-pioneers are shade tolerant species that succeed in moist conditions (Popma *et al.* 1988; Lamb *et al.* 2005). They subsequently continue the succession process by germinating under the cover of pioneer growth since the pioneers provide a low light and moist micro-climate at ground level (Hubbell *et al.* 1999). Non-pioneers may also regenerate from existing plant parts particularly roots, bulbs and other self-generative plant parts (Dietze & Clark 2008).

Forest Gaps are caused by a variety of ways. Some of which are due to natural causes such as tree death due to old age (Eysenrode *et al.* 2000), local levels of pathogenic attacks (Runkle 1981; McCune *et al.* 1988), windthrow (Whitmore 1975; Yamamoto 1992), volcanic and mudflow (Hugget 2004), and vine entrapment (Swayne & Whitmore 1988). These natural determinants create gaps on a relatively small scale, and occurrences randomly distribute throughout the forest stand. Moreover, studies have shown that naturally-caused gaps rarely exceed an area of 100m<sup>2</sup> (Arevalo & Fernandez-Palacios 2007). Because of these frequent natural disturbances, important knowledge on forest species maintenance and diversification may be better understood through species regeneration (Hartshorn 1989), survival (Hubbell *et al.* 1999) and many other aspects of the structure of a viable forest (Runkle 1981).

Anthropogenically induced gaps stringently differ from natural gaps in various aspects, although they are broadly defined as forest gaps. The main anthropogenic disturbance on rainforest stands is induced deforestation. A process which presents itself in an array of forms ranging from all forms of logging (Gondard & Deconchat 2003) land clearing for agricultural, mining and urban development, slash and burning various purposes (Bruner *et al.* 2001). Furthermore, a number of negative effects to ongoing deforestation such as induced flooding and top soil erosion may have also instigated premature tree falls hence forming gaps. These also have negative impacts on the gap regeneration phase, as most naturally dispersed seeds are located within the top soil and hence lost in the process. In addition, soil erosion reduces the fertility of affected areas because most necessities for plant growth forest land remain in the topsoil as results of high turnover of nutrients through continuous decomposing of organic matter on the forest floor (Moran *et al.* 2000).

Gaps resulting from natural canopy perforation caused by death of one or few trees are the kernel of rainforest regeneration (Eysenrode *et al.* 2000) through seedlings already present in the undergrowths, thus forming a building-phase forest (Whitmore 1998). Furthermore natural gaps promote heterogeneity within the forest stands, and possibly bring about high species richness in rainforests (Brandani *et al.* 1988). This latter thought has been described as the "intermediate disturbance hypothesis" which proposed that the highest diversity is maintained at intermediate scales of disturbance (Dietze & Clark 2008). Nonetheless, this remains largely untested for highly diverse rainforest communities, and for the most prevalent patch-size disturbances in such communities as well as for canopy light gaps (Brokaw & Busing 2000). Testing this hypothesis is infeasible due to;



- (i) The longevity of forest species. Data sets large enough to cover temporal and spatial variations of tree species richness and their relationships with disturbances are limited and inconclusive (Gentry 1990; Leopard & Salazar 2008).
- (ii) The mechanisms through which light gaps influence tree regeneration are still not fully expounded (Brokaw & Busing 2000). However, a recent study have shown that alteration of light in wind-throw canopy gaps with shrub growth removed have resulted in a two-fold increase in seed growth and species diversity in gaps (Beckege 2008). This provides evidence that natural gaps could potentially enhance tree diversity given the right microclimatic conditions.

Relatively large gaps are mostly associated with anthropogenic activities (Delegue *et al.* 2000) and other infrequent natural causes such as multiple windthrows (Whitmore 1975; Yamamoto 1992), Earthquake and plate-tectonic movements (Kobayashi 2001), lightning (McCune *et al.* 1988), landslide, volcanism, fire (which is very rare for rainforest) and cyclonic weather on the extreme (Whitmore 1991). These large openings tend to display a rather different route to gap regeneration due to a distinct shift in microclimatic condition near and below the ground as a result in higher influx of electromagnetic radiation (Whitmore 1991). It is this that drives the key disparity in the dynamics of regeneration between “small” and “large” gaps.

Although light is a universally good cue for regeneration (Pompa *et al.* 1988), large gaps have the propensity to do poorly compared to smaller ones due to these two common factors; (i) the lack of ground moisture needed for seed germination and above-ground moisture to maintain seedlings (Xiong *et al.* 2003), and (ii) seed death caused by soil disturbance (Pugnaire & Lozano 1997). The former is strongly associated with the influx in temperature. In high-rainfall areas, excess water in the soil may also inhibit germination. The latter is caused by a range of ways such as; (i) the use of machineries in logging activities and land-clearing that may affect the soil through excavation, trenching and skidding on topsoil, and soil compaction by heavy equipment, (ii) Chemical spillage; for instance, spillage of oil fuels from heavy machineries are common during logging activities, (iii) topsoil erosion and landslide due to flooding, earthquake and volcanism (Whitmore 1991; Yamamoto 1992).

### **Succession and restoration in gaps**

The process of gap succession has been comprehensively discussed in numerous literatures (e.g. Whitmore 1991; Zou *et al.* 1995; Zipperer 2005; Dietze & Clark 2008) having the focal interest on improving the human understanding of factors that might inhibit or promote secondary re-growth. Understanding these, would not only allow for proper actions to be taken to assist the restoration process in extremely degraded gaps, but most importantly, it empowers us with knowledge and skills to manage deforestation in ways that would maximise unaided natural regeneration and restoration in gaps created. However, to begin with, it has been well recognised that a forest community's expenditure in the maintenance of ecological relationships and functions is far less than the cost of recovering from large disturbance such as deforestation. Lu *et al.* (2002) proposed that large scale deforestation leads to losses in biological diversity, alteration of the hydrological cycle, increase soil erosion and loss of productivity. In tropical rainforests, most soils are infertile with a low content of nutrients, making nutrient cycling an important mechanism in maintaining the ecosystem. When the process is disturbed, nutrients can be rapidly lost, and the greater the disturbance on a mature forest, the longer it takes to recover. An extreme situation is when disturbance produces intense degradation with no chance for recovery (Lu *et al.* 2002).

Restoration in gaps is important for the sustainability and livelihood in the forest, but how superior will the restored forest be to the initial stand? There is no universal answer to this question since forest and gap dynamics vary spatially and temporally. In fact, there is no complete homogeneity in forest stands.



However to achieve a good qualitative understanding on how gap dynamics steer the process of regeneration, let us consider four chief sources that; when put together, determines the quality of regeneration in gaps. Let's also be aware of the fact that each of these four factors varies in their role in gap regeneration.

The first factor is the regeneration of pre-existing forest species that have survived following the mechanical phase of disturbance and hence continue to utilize the abundance of light, which was been rather inadequate or just enough for sustainability. These may be climax species which dominated the canopy prior to disturbance, or undergrowths (Denslow *et al.* 1998; Zipperer 2003) waiting for the appropriate environment to flourish. Yet, ramifications of the traditional gap theory for the exclusion of this eminent group are still an issue of debate. Obviously, gap re-growth represents an amalgamation of shade intolerant pioneers and shade-tolerant vegetative developments from existing plants. Yet due to the complexities of vegetation response and the lack of quantified information, non-seed regenerations are typically avoided in the theoretical discussions of gap dynamics (Clark 1991, Loehle 2000; Bond & Midgley 2001). Secondly, the germination from the soil seed bank is vital for gap regeneration and diversification. Studies have shown that this natural process has occurred in forests in response to availability of light (Brokaw & Busing 2001). On the contrary, not all forest stands possess seed banks possible of dormancy for extensive period of time. Evidence of this has been reported by Augspurger (1984) that none of the 18 climax species in Barro Colorado Island had seeds capable of dormancy. The lack of pioneers in the Bornian heath forest is another classic example (Whitmore 1991). It is also important to note that by definition forest gap dynamics would not be applicable to all forest stands as the concept revolves around sapling growth from seed banks. Much is still not known about the temporal and spatial scale of seed-banks in rain forest.

Thirdly, sprouting from cut or crushed roots and stems also play an important contribution in gap regeneration (Dietze & Clark 2008). In such cases where seed bank regeneration does not occur, sprouting re-growth will dominate the gap restoration phase. Therefore it is very likely that species composition at the early gap phase regeneration will resemble pre-existing flora, but having lower flora diversity as not all pre-disturbance species would survive through the disturbance regime. Numerous literatures documented the high rate of damaged flora being a significant part of gap regeneration (Listed in: Dietze & Clark 2008). The fourth source of regeneration is termed 'seed rain,' which is a practical description of how seeds could be brought into a gap via vector- dispersion as animals; particularly birds migrate into gaps for various reasons. Pejchar *et al.* (2008) discussed the impact of birds as a natural means of forest restoration. It was determined that birds use tall trees on gap edges for perching, and that by increasing artificial perches over gaps, bird colonization have increased and so as the seed rain population and diversity, particularly under the perches.

Although forest gaps play an important role in the maintenance of tree species richness in forest communities, or may diversify the forest stand (Tabarelli 1999; Franklin *et al.* 2002), the mechanism maintaining richness of tree species would largely depend on the sources of regeneration as mentioned earlier, the quality and richness of soil, climate conduciveness and other abiotic and biotic factors (Xiong *et al.* 2003). Van Hulst (1992) delineated six possible groups of factors that influence future vegetation through the succession process. These are: (i) Present vegetation, (ii) Present vegetation in surrounding areas or immigration of propagules, (iii) Past vegetation (Dormant seeds), (iv) Present resource levels (light humidity and soil mineral levels), (v) Disturbance level including herbivory and (vi) Stochastic factors such as climate variability and fluctuating supplies of resources. It is rare for a single factor to determine the species diversity and dispersal within gaps, as forest dynamics is a complex array of ecological relationships. However, in comparison with crop plant regeneration in agricultural clearings, forest gap successional vegetation emerges to be better adapted to poor nutrient soils (Lu *et al.* 2002). The dissemination and sprouting capabilities of gap species have also shown a high rate of success in regards to their disturbance intensity and duration (Vieira *et al.* 1996).



### Gap regeneration pathways

Most literature reviewed have agreed to the general notion that tree densities within gaps increase initially, but begin to decline after sometime into the gap-phase regeneration process. Fewer literatures have quantified this further, by suggesting that species decline occurs within 3 to 6 years of gap formation as the trees increase in size (Brokaw 1985; Hubbell & Foster 1986; Runkle & Yetter 1987). It has been a long going interest in forest ecology to determine the mechanisms that would maintain or even enhance species diversity in tree fall gaps (Whitmore 1978, 1989, Runkle 1981, Brokaw 1985, Brandani *et al.* 1988; Denslow & Hartshorn 1994). This has been triggered from the assumption that forest gaps provide environmental conditions driven by abiotic factors (i.e. light, nutrients and space) in which tree species of differing competitive abilities partition heterogeneous resources. However, the empirical support to this notion is poor (Schnitzer & Carson 2001). Besides, some studies even suggest otherwise (e.g. Hubbell and Foster 1986; Uhl *et al.* 1988, Lieberman *et al.* 1995).

Although studies have proposed that gaps do maintain species diversity when reaching climaxity, most of these did not make comparisons between gap diversity and the undamaged forest stand (Hubbell & Foster 1986, Uhl *et al.* 1988, Lieberman *et al.* 1995, Hubbell *et al.* 1999). Moreover, in many Neotropical forests, the early aggressive dominance of lianas should be noted as these pave an alternative pathway in gap regeneration. Liana-dominated gaps remain stalled at a low canopy height for an extensive period. The eventual advancement of regeneration after the long halt has known to result in low species richness in the secondary forest. Paucity of trees in this pathway is revealed to be a function of liana density. Studies carried out in gap-phase regeneration in an old-growth tropical forest on Barro Colorado Island in Panama supported this conclusion (Schnitzer *et al.* 2000). Logged forests are particularly prone to liana invasion (Dawkins 1961; Neil 1984). Subsequent to logging, lianas from the crowns of felled trees can layer and grow rapidly in the gap environment, where they are able to blanket regenerating vegetation and colonize surrounding trees (Gerwing 2001). Hence, due to the high prevalence of lianas in tropical forests (Clark & Clark 1990; Schnitzer *et al.* 2000), the impact of liana on gap-phase regeneration may be highly pervasive, however very little study has been done on the liana-gap regeneration function.

Gaps that are extremely degraded through anthropogenic processes tend to have a low restorative potential due to the active disturbances on the topsoil, thus resulting in the loss of potential seeds and nutrients and other physical, chemical and biological mishaps (Wunderle 1997). In this situation, forest succession maybe greatly mired. If unaided by human assistance, succession would even be incomplete and therefore result in a possible change in the biome structure from forest species to grass or shrub stands, let alone the long temporal scale needed for re-seeding to prevail before succession may then continue. Gaps of extremely large size; though encountering moderate disturbances and retaining a relatively high seed bank, may even proceed through the same fate as formerly described due to the decrease in soil and surface moisture (Breshears & Barnes 1999).

In summary of the above discussion, there are three possible trends in species richness change throughout gap-phase dynamics. First, the widely accepted concept that species richness decline throughout the growth process mainly due to competition for light, nutrients and space (Brokaw 1985). The second line thought describes an opposite trend where liana restricts diversification at the earlier stages of gap regeneration, but after the stalling period, species richness tends to increase virtually from few or none at some cases to a richer flora stand (Schnitzer *et al.* 2000). Once again, various forms of competition and survival factors would determine the climax number. The third trend normally associated with anthropogenic disturbances exhibits a generally low diversity at the initial stages of gap regeneration which prevails throughout the gap restoration. The process may take a large temporal scale if it is to reach climaxity. The latter trend may be even worst affected if liana growth takes over logged areas (Gerwin 2001).



### **Post-disturbance regeneration – A decisive endeavor of human responsibility**

The human impact on the natural environment over the last century has been horrendous. Tropical forest biomes are rapidly disappearing in the name of social and economic demands but little has been done to address the problem over the years (Lamb *et al.* 2005). The point of present interest is; whether human tailored restoration programs are capable in transforming a degraded forest systems into a viable phase of high species regeneration that has the capability to produce an equivalent or superior forest composition with better adaptability to temporal changes in the environment. Anthropogenic disturbances; though how petite or colossal they may be, still instigates the problem of regeneration and restoration. In the few past years, researchers have been committed to determining alternatives to encounter the problem of forest degradation. From these efforts, new forms of reforestation techniques have been developed for tropical forest landscapes which have shown a wide success. These include improvements in the management of secondary or regrowth forests as well as more complex forms of reforestation where forest cover has been entirely lost (McDonald 2004).

It is evidently clear that flora diversity restoration can be improved by the careful location of protected areas within previously disturbed locations (Margules *et al.* 2002). It is also vital to include adjacent undisturbed forest areas in the protected zones as to provide seed sources and dispersal vectors for the disturbed areas. However this method is only workable for areas where not all degraded land has been deforested hence leaving fragmented patches of forests capable of producing seeds that would then be vectored into cleared areas by animals or natural dispersal processes. Without proper protection, the further use of cleared land could inhibit the effectiveness of the natural re-vegetation process. Natural recovery of degraded forest areas is however not predictable although protection is put in place to ensure that the process persists. Recovery is stalled when the system has crossed an ecological threshold thus inhibiting the perseverance of forest species (Hobbs *et al.* 2006). Regeneration at this point can be described as reaching a new steady state condition (Lamb *et al.* 2005). A common example is when degradation leads to topsoil loss and a reduction in soil fertility, complicating recolonization of these sites for many of the original species, thus surviving species richness would be extremely low. Another threshold is commonly crossed when sites become occupied by grasses and other invasive non-forest species. This increases the risk of wildfires, particularly in the seasonal tropics, which then reduces woody plant recruitment and favors the further spread of grasslands (Lamb *et al.* 2005). There are many examples throughout the tropics of extensive grasslands that persist over time despite being entirely surrounded by forests (McDonald 2004).

In cases where unaided recovery is not possible in degraded forest land, a number of ways have been actively used to address the situation. In the traditional mind set, it is always the goal of restoration to re-establish the original forest ecosystem. However, the rules of ecosystem assembly still remain unsettled (Fukami *et al.* 2005). Lamb *et al.* (2005) pointed out two broad approaches which flora diversity can be restored via human effort. These steps are centered on the concept of restoration through planting. Though an expensive and in some cases an extent exercise, restoration planting have been proven successful in many empirical studies. Firstly, restoration plantings using small number of short-lived nurse trees. These light demanding trees serve as pioneer species that shade off non-forest species such as grasses and other possible unwanted competitors and therefore provide a conducive microclimate for the establishment of the secondary forest species, some of which lay dormant on the top soil awaiting the right conditions for germination and then growth. Secondly, restoration plantings using large number of species from later succession stages. This would increase the chance for high diversity in the climax stand. In situations where seed banks do not consist of secondary species, this method ensures that the later succession stages are reached, however in this circumstance the climax stand would be wholly determined by the artificially disseminated seedlings which may, or may not resemble the pre-existing forest stand depending on the selection of seed source. There may also be seed rain coming through from nearby forest stands that would benefit from the pre-grown shade trees.



A third approach is termed direct seeding, and is different from the previous two as it requires a much greater number of species representative of more mature successional stage (Lamb *et al.* 2005). Planting are usually at high densities *e.g.* 92500 trees per hectare (Parrotta & Knowles 1999). The climax forest stand depicted in this approach is practically a function of the competitive interaction between the seedlings at the mature successional stage. Ideally, this approach resembles a degraded forest land with an initial seed bank that given the appropriate conditions undergo the regeneration process. The number of species that can be established by direct seeding is limited by seed supply but the establishment cost can be lower. Direct seeding can be used to initiate reforestation in open fields under appropriate conditions but it may be most useful when used to enhance diversity once some tree cover is already present (Lamb *et al.* 2005). This approach is not as versatile as those previously discussed as conditions needed for initial germination are narrowly specific since most seeds only germinate and dominate the late successional stages.

## CONCLUSION

Forest gaps (despite their sizes) are all results of various forms of disturbances to the forest canopy and stand. It is the forest's natural response to repair itself from these inflicted damages however, the biological and mechanistic response in this repairing process is monotonous in a sense that plants do not weigh out the intensity of disturbance before responding. Regardless of the amount of disturbance endured, the natural response is always a steady means of getting back to climaxity. Naturally caused gaps are most likely to recover through the gap-dynamic processes which not only rely on regeneration through seedlings but also through regrowth of damaged and pre-existing flora. This has been the natural process that has allowed forest structures to evolve over time, hence tolerating climatic shifts over large temporal scales.

Self-restoration is not always plausible, especially in relatively large gaps formed by anthropogenic activities. In such context, human effort is needed to ensure that the restoration process is initiated. Three relatively broad approaches were proposed to provide the only hope in restoring large gaps of open land and badly damaged forest stands. Until further alternatives are tested and proved effective, the three approaches remain paramount in restoration ecology. However, the biggest challenge will be transitioning the approaches from a site-based activity to an extensively large landscape application. The success of the approaches on a landscape level would certainly result in the restoration of biodiversity (Lamb *et al.* 2005). A huge potential lies ahead in converting degraded land into new forest stands. Nonetheless, only until the results are available from ongoing pioneer work can we endorse or reject the notion that anthropogenic induced gaps can be a blessing in disguise, as it drives mankind to solve ecological problems of their own making. And better still; through these efforts a better understanding of the key players in ecological processes in forest communities would be achieved.

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