Long-term fragmentation effects on the distribution and dynamics of canopy gaps in a tropical montane forest

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Abstract. Fragmentation alters forest canopy structure through various mechanisms, which in turn drive subsequent changes to biogeochemical processes and biological diversity. Using repeated airborne LiDAR (Light Detection and Ranging) mappings, we investigated the size distribution and dynamics of forest canopy gaps across a topical montane forest landscape in Hawaii naturally fragmented by lava >100 yr ago. The combined effects of long-term isolation were evaluated using edge-proximity patterns in the distribution of gaps identified in year 1 ("existing gaps"). In addition, using the data from year 2, we investigated patterns in the loss of canopy ("new gaps") and regrowth of canopy ("filled gaps"). The size distributions of the three gap types were modelled using the power-law exponent, λ. We found that fragmentation has resulted in some large changes in gap dynamics, with both the total area of gaps and the relative proportion of large existing gaps increased with distance to fragment edge. In models of power-law distribution scaling, λ estimates decreased to asymptotic values within 20 m of fragment edges for existing gaps. The size distributions of new and filled gaps were surprisingly similar. However, the total area of filled gaps was less than that of new gaps, and this difference was greatest near fragment edges. From these results, we conclude that fragmentation may be capable of continuously altering gap-phase dynamics of a forest for more than a century.

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INTRODUCTION

Tropical forests play an important role in the regulation of biospheric and atmospheric processes, and they harbor a large portion of Earth's biodiversity (Mittermeier et al. 1998, Gardner et al. 2009). The functioning of these forests and the various services they provide are highly affected by human activities (Gardner et al. 2009). Of these activities, fragmentation is the most common and, with respect to impacts on forest function and ecosystem services, potentially the most influential. Fragmentation is occurring on a global scale, and a large number of studies have shown that this disturbance has both immediate and long-term effects on biodiversity (Krauss et al. 2010, Morris 2010) and on forest structure and function, especially near forest edges (Harper et al. 2005, Broadbent et al. 2008). Accordingly, as forests become increasingly fragmented, their ability to provide habitat and to regulate global processes such as energy and hydrological cycles will diminish (Terborgh and Terborgh 1992, Laurance et al. 1998*b*). Despite the significance

of this disturbance type, very little is known about the effects of fragmentation over longer (centennial) time scales (Vaughn et al. 2014).

One pathway by which fragmentation affects forest biodiversity and function is by altering the natural processes of gap formation and gap filling. In forests that have reached a mature state, including tropical forests, a stable rate of forest canopy gap formation and filling is expected (White 1979, Hashtorn and Hartshorn 1980). These gap-phase dynamics are important to consider for several reasons. Through modification of the light environment, the sizes and spatial arrangement of gaps influence plant community composition as well as carbon dynamics (Brokaw and Scheiner 1989, Canham et al. 1990, Denslow et al. 1998, Yamamoto 2000, Espírito-Santo et al. 2014a). Larger canopy gaps affect local tree diversity and growth by creating a light environment that favors light-demanding species (Chambers et al. 2009). Smaller gaps, while not as strongly linked to overstory biodiversity (Hubbell et al. 1999, Brokaw and Busing 2000), are regulate understory floral and faunal biodiversity (Levey 1988, Denslow et al. 1998, Schnitzer and Carson 2000).

To accurately describe the gap-phase dynamics for a forest, gaps of all sizes must be considered (Brokaw 1985). Resulting data sets are large and complex for even structurally simple forests, but probability distributions of gap area can be used to rapidly quantify and convey gap data. Because smaller gaps are exponentially more likely to occur than large gaps, these distributions generally follow a simple power law (Kellner and Asner 2009). Under such a distribution, the relative occurrence of small versus large gaps is represented by a single parameter (usually abbreviated as λ). The value of this parameter is determined by the frequency and type of disturbances that occur (White 1979, Romme et al. 1998), which are in turn affected by forest composition, climate, and underlying geologic conditions (Phillips et al. 2004, Kathke and Bruelheide 2010). Due to the extreme rarity of larger gaps, it is difficult to quantify this distribution over large scales relying on strictly ground-based field approaches (Fisher et al. 2008, Asner 2013). Remote sensing allows for the spatial sampling of gaps over areas large enough to capture the patterns and processes related to gap dynamics, and several studies have used remote sensing successfully for this purpose (Nelson et al. 1994, Chambers et al. 2009, Kellner and Asner 2009, Kathke and Bruelheide 2010, Espírito-Santo et al. 2014b).

Such gap distributional analyses have been conducted over large areas of intact forest, yet to date, there is little knowledge of how fragmentation and fragment size affect forest gap dynamics. This is especially true in montane tropical forests, where disturbance regimes and gap dynamics remain very poorly known (Asner et al. 2014). Addressing this issue is also difficult because many fragmentation studies are confounded by continued human use of fragments, which can cause changes to forest structure independent of fragmentation events, a new matrix, and physical variables (e.g., soil fertility) that drive clearing in one area and not another (Ewers and Didham 2006). These are critically important concerns because accurate characterization of fragmentation effects on gap distributions requires large land areas, long periods of time since isolation, and an absence of such confounding factors.

To address these issues, we took advantage of a large, naturally occurring array of forest fragments on the northeastern slope of Mauna Loa volcano on the island of Hawai'i, a model study system for understanding the effects of long-term fragmentation on forests (Morden and Loeffler 1999, Vandergast and Gillespie 2004, Flaspohler et al. 2010, Vaughn et al. 2014). Our goal was to use airborne Light Detection and Ranging (LiDAR) data to quantify and understand the effects of fragmentation and fragment size on canopy gap structure of tropical montane forests. Using LiDAR acquired in two consecutive years, we mapped and analyzed existing forest canopy gaps present in the first data acquisition, the new gaps that formed between the two years of observation, as well as the regions of existing gaps that filled in during the two years. In previous work in this model study system, we found that forest fragment size and shape combine to influence forest canopy structure (Vaughn et al. 2014). Specifically, canopy height and canopy depth decrease, while gap fraction increases at fragment edges, with the magnitude of each effect dependent upon distance to a fragment edge, as well as the amount

of surrounding fragment area. Based on this insight, we addressed two new questions: (1) Does fragmentation of montane tropical forest alter the size-frequency distribution of canopy gaps? (2) Are changes related to fragmentation still unfolding after more than a century of isolation? We hypothesized that the fragmentation event initiated a shift of the remnant forest fragments toward smaller gap sizes, that fragment edges are most affected, and that these fragments are still exhibiting the effects of these shifts in year-to-year changes in gap creation and regrowth.

METHODS

Study area

The study area is located within the elevation range 1400–2000 m on the northeast face of Mauna Loa, the Earth's largest volcano (Fig. 1). In the years 1855 and 1881, the study site was affected by two lava flow events. These flows entered previously intact forest on 3000- to 5000-year-old substrate (Sherrod et al. 2007), and created >1000 forest fragments, ranging in size from <0.1 to >200 ha, each embedded in a matrix of minimally vegetated lava rock. In addition to extensive replication in two highly isolated events, this study system has several other attributes that make it a model study system for studying ecological responses to fragmentation. Hawaii's extreme isolation has kept the canopy species composition relatively simple. The dominant canopy species is *Metrosideros polymorpha* (ohia), an evergreen tree endemic to the Hawaiian Islands. Another endemic species, *Acacia koa* (koa), occurs in the canopy along with *M. polymorpha*, but in much lower abundance. There are also a limited number of dominant mid-story and understory plant species: *Cheirodendron trigynum* (olapa), *Cibotium glaucum* (hapuu), *Coprosma montana* (pilo), *Ilex anomala* (kawau), and *Myrsine lessertiana* (kolea), and these are common across fragments (Flaspohler et al. 2010). These forests have also experienced protection in the form of forest reserves, and because of difficult access, have never been actively managed.

LiDAR data collection

On 10 and 13 January 2008 the Carnegie Airborne Observatory (CAO; http://cao.carnegiescience.edu) Beta system (Asner et al. 2007) was flown over the area at a height of 2500 m above ground level at an average speed of 75 knots. The CAO-Beta LiDAR system had a laser beam divergence of 0.56 mrad (1/e) and a laser wavelength of 1064 nm. For this data collection, we used a LiDAR pulse frequency of 33 kHz, a scan frequency of 10 Hz, and a half-scan angle of 17.5 degrees. Swath overlap was nominally 35–40%. Up to four discrete returns per pulse were recorded. These flight and instrument settings yielded a dataset of 1.17 returns per m^2 on average over the vegetated areas. The following year on 12 January, the CAO returned to the same area to do a second survey. During this second data acquisition, we used a flight altitude of 2000 m, a flight speed that averaged 80 knots, a pulse frequency of 50 kHz, a scan frequency of 20 Hz, and a half-scan angle 19 degrees. Under these settings, the resulting point density was about 1.88 returns per m^2. LiDAR spatial error under this system was previously determined to be <0.15 m vertically and <0.36 m horizontally (RMSE; Asner et al. 2010).

The LiDAR data from 2008 and 2009 were used to create models of top-of-canopy height within the study region. We first created a single reference ground digital surface model (DSM) from the higher resolution 2009 LiDAR collection. First, all returns from the 2009 LiDAR collection were classified as ground or vegetation returns using the lasground program of LAStools (RapidLasso, Gilching, Germany). Next, using the las2dem program of LAStools, a triangulated irregular network (TIN) was constructed from these ground returns and interpolated into a DSM raster image with a resolution of 1 × 1 m. We then used a similar process to build a DSM of the canopy surface each year. For these models, a TIN was constructed from the first returns of all LiDAR pulses, irrespective of the ground/vegetation classifications of the returns. These canopy surface TINs were then interpolated to DSM raster images along the exact same 1 × 1 m grid used for the ground DSM. To further reduce the effects of inter-year variation in LiDAR collection we further reduced the resolution DSM models to 2 × 2 using a mean filter. This step greatly reduces errors in the canopy surface model that may arise when a LiDAR pulse passes directly
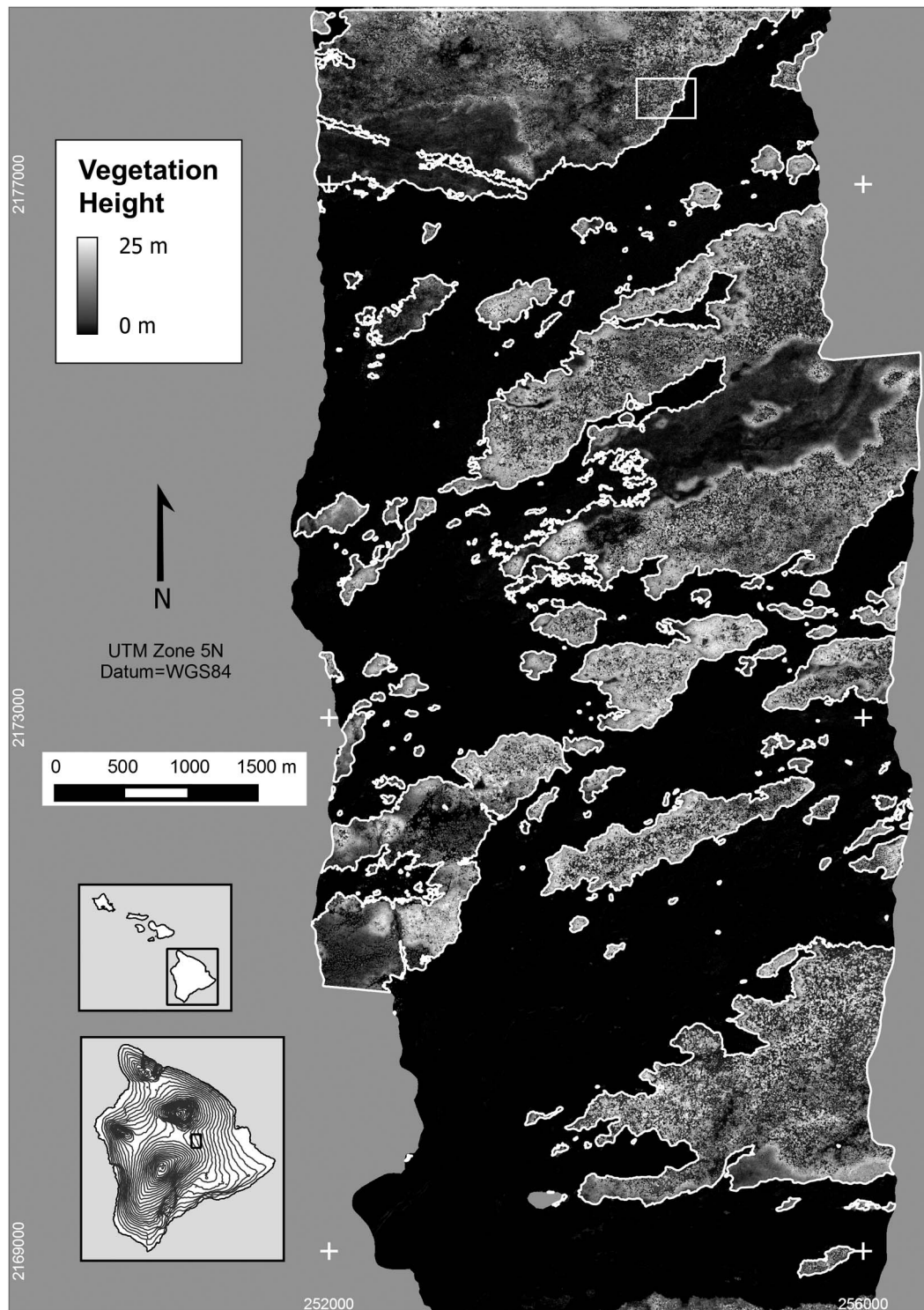
Fig. 1. The study area from which gap characteristics were computed from LiDAR mapping in 2008 and 2009. Brightness indicates canopy height, so forested fragments can easily be seen amongst the lava-substrate matrix. The framed area appears in Fig. 2.

between two adjacent branches that would otherwise be considered gapless. Finally, for each year, we computed a canopy height raster model by subtracting the vegetation surface (DSM) from the reference 2009 ground DSM.

Fragment boundaries

We used a previously created set of fragment boundaries for the study area (Vaughn et al. 2014). The boundaries were created using a combination of the 2008 LiDAR-derived canopy height data and an associated Normalized Difference Vegetation Index NDVI dataset derived from the imaging spectrometer aboard the CAO aircraft (Asner et al. 2007). The methodology is fully described in (Vaughn et al. 2014). Using Gaussian-smoothed maps of these variables, forest fragments were delineated using two criteria: canopy height > 3 m, and NDVI > 0.7. All cells meeting these criteria were marked, and boundaries were established around all connected clusters of marked cells. Clusters with area >0.02 ha (200 m^2) were considered unique fragments, and they were kept for further analysis. Because the boundary locations were created from smoothed canopy height data, the resulting fragment areas were slightly larger than the actual fragment area. To correct for this, we shrank the boundary of each of the forest fragments by 2 m inward along the entire perimeter.

Gap detection

Within the forest fragments in the sampling area, gaps in the canopy height models were detected as contiguous regions in the canopy height map that met certain conditions (Fig. 2A). A polygon was drawn around the perimeter of each detected gap in the study area, and we used the computed area and the centroid point of these polygons as the size of the gaps and the mapped gap locations, respectively. The minimum size of an identified gap was 1 cell, or 4 m^2. Additionally, the distance between centroid and the nearest fragment edge was computed for all gaps.

Three kinds of canopy gaps were identified using a threshold of 2 m above ground, which corresponds with the definition of a canopy gap in Brokaw (1982). "Existing" gaps were those that already existed at the time of our 2008 LiDAR data collection. These were identified as regions of the 2008 canopy height model that fell below the 2 m threshold (yellow areas in Fig. 2A). "New" gaps were those representing additional losses of canopy that formed between 2008 and 2009. These were regions that had canopy height above the threshold in 2008 and below the threshold in 2009 (orange areas in Fig. 2A). "Filled" gaps are regions of existing gaps that regrew between the two measurements, and are the opposite of new gaps. These were regions which had canopy height below the threshold in 2008 and above the threshold in 2009 (yellow areas in Fig. 2B). Note that existing gap may fill on multiple edges simultaneously, and under this methodology, more than one filled gap could be detected within the boundary of a single existing gap. To detect the formation of new gaps and filled gaps, it was required that the sampling area be limited to the overlapping area of both the 2008 and the 2009 LiDAR point data coverage (Fig. 1). To be able to compare all three gap size distributions, the same sampling area was used for all three gap types.

Gap-size distributions

Differences in gap distributions were first analyzed by summing areas of gaps. First the total area of gaps was simply the number of cells in the study area that were within fragments and identified as a certain gap type. Next the region was then divided into intervals of distance-to-edge, and the total cell area of each gap type within each distance interval was divided by the total cell area in the distance interval to get a proportional area of each gap type. The total cell area of each gap type within each distance interval was further broken down into intervals of gap size, giving a first glimpse of changes in gap size distribution along distance to fragment edge.

In a second analysis, we fit the data to a power-law gap size distribution. Two models were used depending on the functional relationship between the scaling parameter, λ, and distance-to-edge. The first model was no relationship, or a constant λ:

$$\lambda = \beta_0 \qquad (1)$$

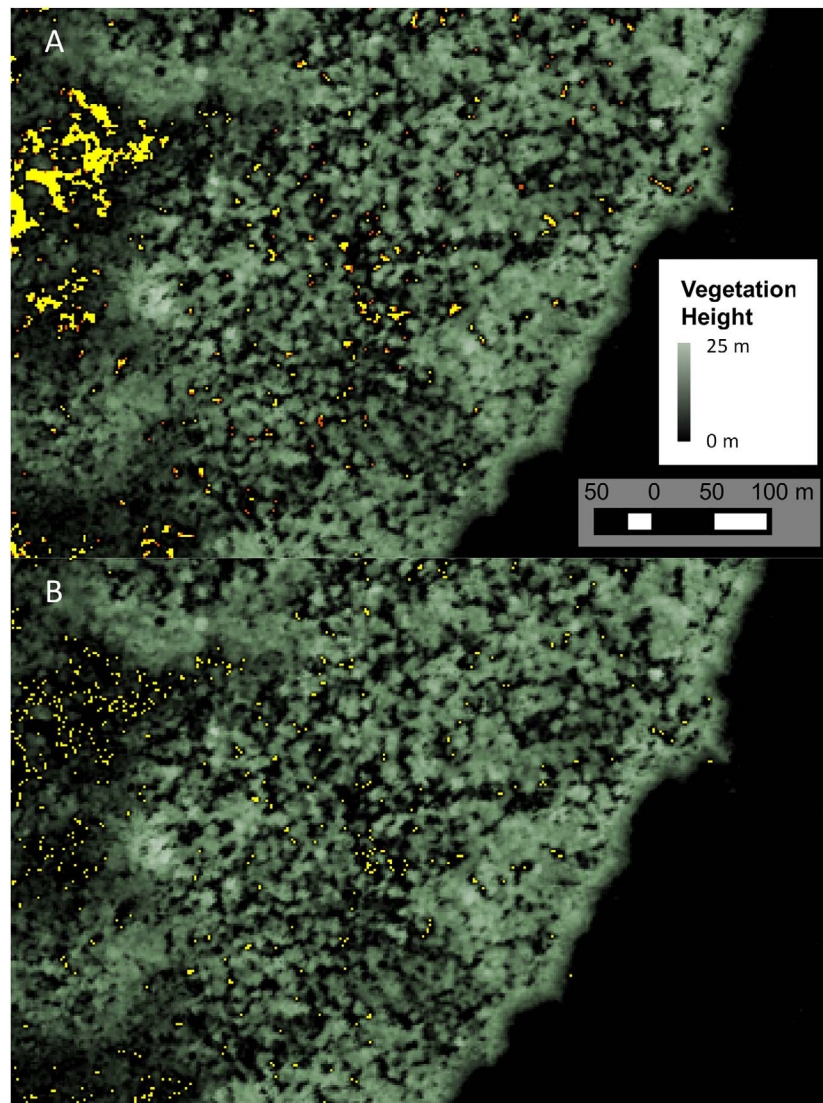A second model included distance-to-edge as a determinant of λ. After exploring more complex

Fig. 2. Examples of gap identification from the canopy height maps. Using a 2-m canopy height threshold, three types of gaps are identified. Panel (A) shows those existing at the time of the first LiDAR acquisition in 2008. Yellow regions remained gaps in 2009. Orange regions are filled gaps, which are portions of existing gaps that grew above 2 m before 2009. Panel (B) shows new gaps which were created between 2008 and 2009 in yellow.

functions with more flexibility, we found that a simple three-parameter exponential function with an intercept term (Eq. 2) was sufficient for the data:

$$\lambda = \beta_0 + \beta_1 e^{-\beta_2 \log d} \qquad (2)$$

with d as distance-to-edge in meters from gap centroid to fragment boundary.

Gap sizes in our study were drawn from raster cell counts, requiring the use of a discrete-valued distribution. The Zeta distribution is a discrete version of the Pareto distribution

$$f(k) = \frac{k^\lambda}{\xi(\lambda)} \qquad (3)$$

with $\xi(\lambda)$ referring to the Riemann zeta function, where k is any positive integer, and λ is constrained to positive real numbers greater than unity. Under this distribution the value of λ is akin to the slope of the relationship between log
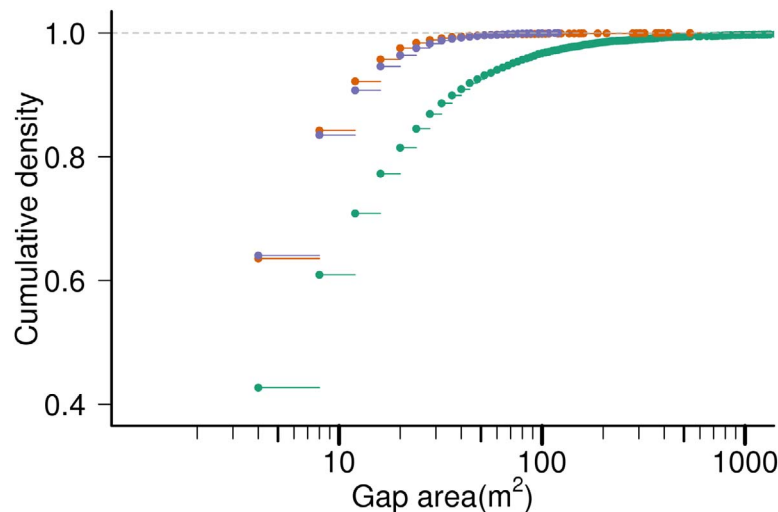
Fig. 3. The cumulative distribution of log-transformed size of existing 2008 gaps (green), new gaps created between 2008 and 2009 (orange), and gaps filled between 2008 and 2009 (purple). While the distribution of new gaps nearly matched that of the existing gaps, the filled gaps tended to be much smaller in area.

frequency and log size, and λ increases with the ratio of smaller to larger gap sizes. This representation has proven useful in previous studies (Kellner and Asner 2009). All models were fit to the full collection of identified gaps of each type using a basic maximum likelihood approach, where likelihood was computed using the Zeta distribution in Eq. 3. Eq. 2 allows λ to decrease at a variable rate determined by the distance-to-edge while approaching an asymptotic minimum value at a sufficiently large distance. The effectiveness of using the two-parameter functional model over the constant model was tested using a standard log-likelihood ratio statistic compared to the Chi-squared distribution with two degree of freedom. Akaike's Information Criterion values were also computed for each model for comparison.

Under Eq. 2, a value of parameter β_2 near zero would indicate that distance-to-edge is ineffective at determining λ and that the model of constant λ would be more appropriate. Thus to further assess the separation of distribution of the model parameters, we used a bootstrap procedure to estimate the sampling distribution of the model parameters for each gap type (Efron and Tibshirani 1993). For each of 512 iterations, the dataset for each of the three gap types was resampled with replacement to match the original number of gaps. In each iteration, the maximum likelihood estimation procedure was performed to obtain a new bootstrap parameter set β^*, and the collection of 512 such bootstrap parameter sets forms an empirical approximation of the actual sampling distribution of each parameter of interest. We used these approximations to assess both the stability of all model parameters and the difference of β_2 for each gap type from 0.

RESULTS

In the area of overlap between the 2008 and 2009 LiDAR imagery we identified 320 forest fragments greater than 0.02 ha in size. The majority (68%) of these were smaller than 1 ha. Of those remaining, 23% were 1 to 10 ha, 5% were 10 to 100 ha, and 3% were >100 ha. Together, these fragments contained 12642 existing canopy gaps, 17394 new gaps, and 13559 filled gaps with a minimum area of 4 m^2. Thus, on average, more than one region of a single existing gap filled in during the one-year period. The total area of these gaps was 46.8 ha, 12.5 ha, and 9.8 ha, or 2.14%, 0.57%, and 0.45% of the forest area, respectively. Thus, new and filled gaps were generally smaller compared to existing gaps, and their size distributions were very similar (Fig. 3). The number, area, and variation in gap size across the entire study area were large
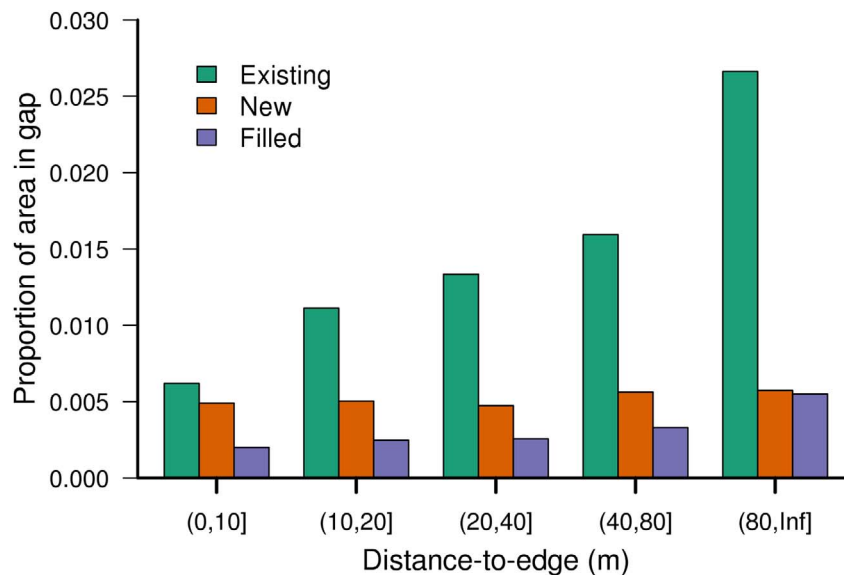
Fig. 4. Proportion of the total study area that was identified as gap, after dividing the region into intervals of distance to fragment edge: 0 to 10 m, 10 to 20 m, 20 to 40 m, 40 to 80 m, and >80 m, and into gap size intervals: 0 to 10 m^2, 10 to 50 m^2, 50 to 100 m^2, and >100 m^2. Separate bars show the existing 2008 gaps (green), new gaps created between 2008 and 2009 (orange), and gaps filled between 2008 and 2009 (purple).

enough that we were able to construct a well-populated power distribution of the gap sizes. The distributional differences in gap types were also demonstrated by the estimated site-wide constant λ values (Model 1) of 1.363 for existing gaps, 1.444 for new gaps, and 1.442 for filled gaps. No evidence was found that the distributional similarity of new and filled gaps was the result of positional error between the two LiDAR datasets. Such errors would appear as moving trees, resulting in new gaps on only one side of trees, or would cause new gaps and filled gaps to occur on opposite sides of existing gap openings.

We found differences due to position within fragments in the total number of gaps and the apportioning of gaps into size intervals. For existing gaps, the average gap size increased from 8.7 m^2 within 10 m from fragment edge to 33.3 m^2 for gaps located between 20 and 40 m of edge. The amount of the study area identified as existing gap quadrupled from 0.6% to 2.7% as distance-to-edge increased (Fig. 4). In addition, the relative proportion of large and small existing gaps sizes was markedly different in edge regions, with far less of the total gap area made up of larger (>100 m^2) gaps (Fig. 5). Similarly, the amount of filled gap area increased with

distance-to-edge, though not nearly as quickly as with existing gaps (Fig. 4). Large filled gaps were also slightly more common in interior areas (Fig. 5). In contrast, the total proportion of new gap area was nearly constant at about 0.5% across all distance-to-edge intervals (Fig. 4), and there was little shift found among the various new gap size classes across the same gradient (Fig. 5).

When we modelled λ for existing gaps using distance-to-edge, we found that model 2 was a significant improvement over the constant-λ model 1. For the existing and filled gap types, the p-value and AIC values both indicated that distance-to-edge is an important driver of gap size distribution (Table 1). This was not true for new gaps, which showed little response to distance-to-edge. In addition, the bootstrap distributions of β_2 for all three gap types contained no values less than 0 (Fig. 6D–F). However, there were some values relatively close to 0 for new gaps, and the parameter estimate using the full dataset fell into this region (red line in Fig. 6H). In some cases, these distributions were slightly skewed, and especially for filled gaps, this skew appeared to be from correlation between β_0 and β_1. The penetration depth of the effect of distance-to-edge varied by gap type, and was
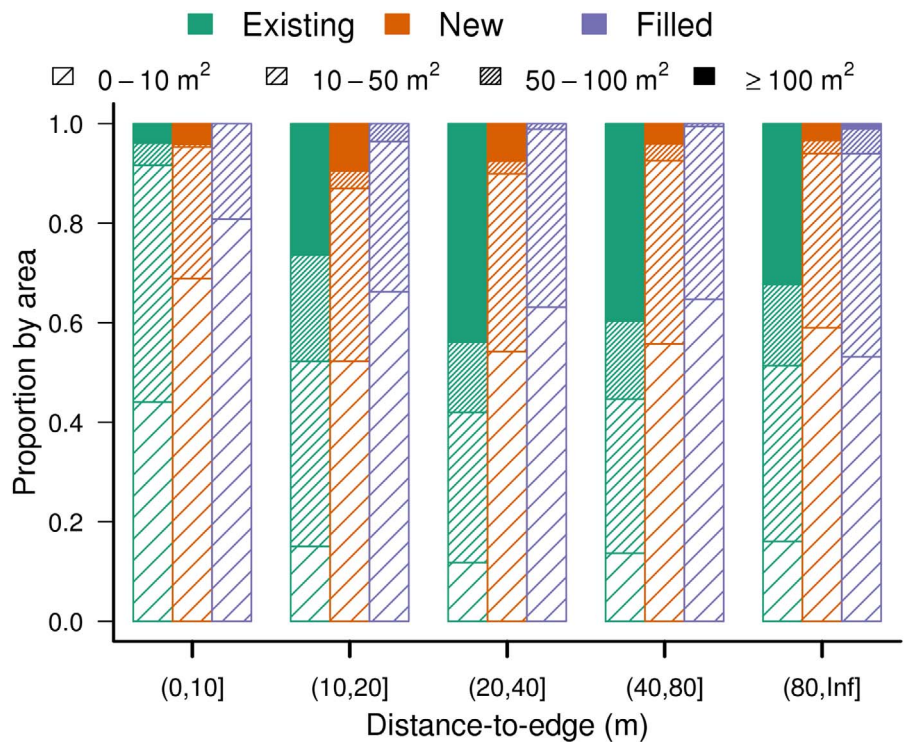
Fig. 5. A breakdown of the total area of gap in the study region, for existing 2008 gaps (green), new gaps created between 2008 and 2009 (orange), and gaps filled between 2008 and 2009 (purple). The total area of gaps was first divided into intervals of distance to fragment edge: 0 to 10 m, 10 to 20 m, 20 to 40 m, 40 to 80 m, and >80 m. Then the area within each of these distance intervals was proportionally divided into bins of individual gap size (horizontal area): 0 to 10 m^2, 10 to 50 m^2, 50 to 100 m^2, and >100 m^2.

greatest (up to 100 m) for filled gaps (Fig. 7). For new gaps the effect of distance-to-edge reached only about 5 m into fragments. The total shift in estimated λ (from >2 to about 1.35) was greatest for the existing gaps (Fig. 7).

DISCUSSION

After more than a century of isolation, the fragments of tropical montane forest in our study area contained a very high number of large-sized treefall gaps. The site-wide λ estimate of 1.36, is much smaller than has been reported for other tropical forest sites in Hawaii and South America (Boyd and Danson 2005, Kellner and Asner 2009, Lloyd et al. 2009, Asner et al. 2013). While the scaling parameter may be sensitive to the exact methodology used (e.g., gap height threshold selection in Kellner and Asner [2009]), some features of this study site could also have led to

Table 1. Results for the model of nonconstant λ (model 2) for gaps existing in 2008, new gaps that formed between 2008 and 2009, and gap regions that filled in during the same two years.

Gap type	β_0	β_1	β_2	LL ratio†	p‡	AIC_0	AIC_A
Existing	1.353	0.749	1.719	49.3	1.97×10^{-11}	108524	108479
New	1.430	0.021	0.102	0.37	8.30×10^{-1}	124410	124414
Filled	0.921	0.581	0.022	15.31	4.73×10^{-4}	97391	97380

Note: AIC is Akaike's information criterion, 0 = null model, A = full model.
† Log-likelihood ratio versus model 1 (constant λ).
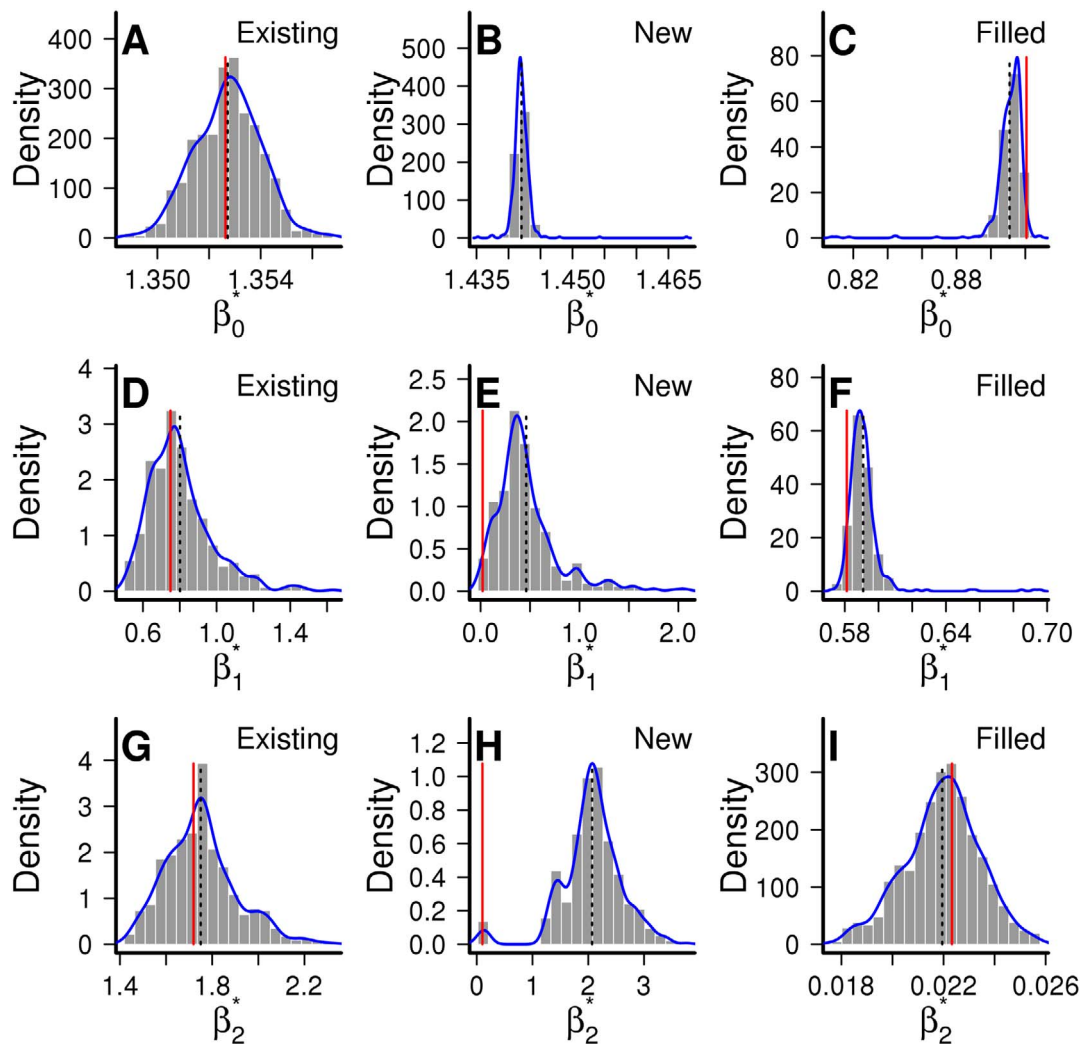‡ Approximate, taken from a chi-squared distribution with 2 degrees of freedom.

Fig. 6. Bootstrap parameter distributions of the two-parameter model of λ as a function of distance to fragment edge, using existing 2008 gaps, new gaps created between 2008 and 2009, and gaps filled between 2008 and 2009. The dashed black line is the mean value from the bootstrap procedure. For comparison, the values of each parameter determined from fitting the model to the full dataset are shown in red.

an increased rate of large gap creation. First, because of its young age, the substrate (approx. 3000 to 5000 years old; Sherrod et al. 2007) provides limited available forms of nitrogen and phosphorus (Chadwick et al. 1999). This factor, combined with the site's moderate elevation, results in slow growth rates (Raich et al. 1997). Smaller gaps may be filled more rapidly with new influx or recovery of vegetation in comparison to large gaps, and slower growth rates would only increase the disparity between the residence times of small and large gaps. Second,

higher wind speeds have been found at the elevation of the site (Juvik and Nullet 1994), and this could drive a larger number of treefall events. More generally, forest edges can increase wind speeds and increase the risk of tree fall (Mitchell 1998), and this is certainly a possible driver of increased presence of large gaps at this site.

In addition to forming more readily, the montane environment may slow the rate of gap regrowth. Of note is that many of the smaller new gaps occurred on the edges of existing gaps,
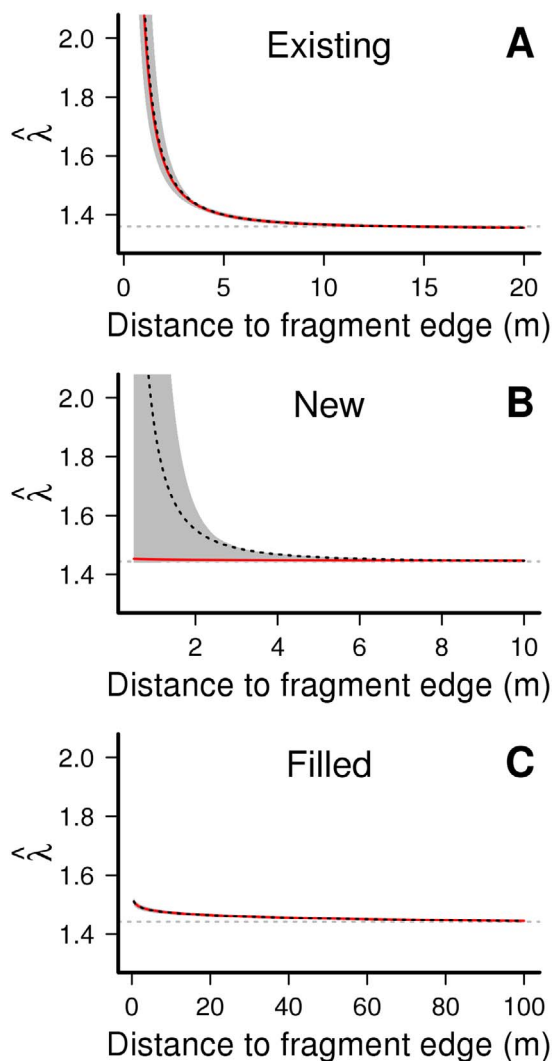
Fig. 7. Estimated λ as a function of distance to fragment edge for existing 2008 gaps (A), new gaps created between 2008 and 2009 (B), and gaps filled between 2008 and 2009 (C). Grey regions show the full range of λ when estimated using the 512 bootstrap parameter sets. The red solid line is the output from model 2 applied to the full dataset. The dashed black line is the output from model 2 using the average parameter values from the bootstrap procedure. A gray dashed horizontal line at the estimate of β_1 from model 1 (constant λ) is plotted for reference.

a contagion like effect of disturbance begetting disturbance that has been observed elsewhere (Young and Hubbell 1991, Jansen et al. 2008, Lertzman et al. 2014). However, because of the lack of similarly detailed and large scale data from other fragmented systems, whether this is occurring at a rate that is unique to Hawaiian montane forests in unknown. Because larger gaps require even more time to fill, there may be increased opportunity for woody plant species with multiple growing strategies to enter the site (Denslow 1987, Levey 1988, Laurance et al. 1998a, Brokaw and Busing 2000). However, considering the location of this study system in Hawaii, longer-lived large gaps may also result in more complete invasion by non-native plant species. If invasive species were to establish, this could alter structure and reduce native biological diversity (Williamson 1999, Asner et al. 2008).

Despite the increased proportion of large gaps at our site compared to other regions of the world, the demographics of existing forest canopy gaps at fragment edges were notably different from those of fragment interiors. We found that both the total area of all gaps (Fig. 4) and the average area of individual gaps were reduced at fragment edges compared to fragment interior. Indeed, gaps larger than 50 m^2 were hardly present at fragment edges (Fig. 5). Thus, the canopy at edges is more spatially uniform than in the interior. At this same location, both total canopy height and canopy depth were found to increase with distance-to-edge (Vaughn et al. 2014). In this context, the observed differences in gap size demographics make sense, as shorter trees tend to make smaller gaps when they fall (van der Meer and Bongers 1996). The shorter, more uniform canopy and the more limited number of larger gaps indicate that the canopy at fragment edges is functioning in a similar manner to that of a much younger forest.

The shifts in canopy structure and gap size frequencies at fragment edges also lead to differences in the light environment and habitat value of these regions. Large differences in environment often occur between fragment edge and forest interior (Matlack 1993, Laurance et al. 2002, Harper et al. 2005, Broadbent et al. 2008). At this study site, we previously observed that light passing through the canopy increases with proximity to fragment edges (Vaughn et al. 2014). This is in line with other observations that the total canopy cover is often smaller at forest fragment edges (Chen et al. 1992, Kapos et al. 1993). However, in this study we found that the

total area of existing gaps increased with distance-to-edge (Fig. 6). Thus, the interior canopy is patchier, but its taller and thicker stature results in a less light reaching the forest floor on average. At our study site, the existing gap distribution stabilized within 20 m of the edge of the fragments, a distance similar to that for canopy height, vertical depth and gap fraction, which stabilized 20 to 50 m from the fragment edge (Vaughn et al. 2014).

By identifying new gaps in addition to already existing gaps, we found that after more than a century, fragmentation events may no longer be affect gap creation rates. The model of λ for new gaps did not show a significant effect of distance-to-edge, and the response depth was less than 5 m into fragment interiors (Fig. 7). Similarly, the proportional area of new gaps was constant across levels of distance-to-edge (Fig. 4). Thus, with respect to edge proximity, new gaps formed almost entirely at random. This strongly suggests that the effects of fragmentation on gap forma-tion may have stabilized in the past century. While not directly comparable to gap area rates, published tree mortality rates in tropical forest world-wide range from 1% to 3% yr^{-1} (Phillips et al. 1994, Condit et al. 1995, Lieberman et al. 1995). In this context, the 0.5% of the forest canopy in the study area that converted to gap between 2008 and 2009 is not exceptional.

While rates of tree loss have decoupled from the influence of fragment edges, the same may not be true for rates of gap regrowth. Because new and filled gaps result from opposing processes, it was surprising that the two distri-butions were so similar. However, there were important differences in the total amount of new and filled gaps. Summed across the entire region, total area of filled gaps was smaller than that of new gaps, resulting in a total net loss of canopy of about 0.12%. Thus, for this one year timespan the formation of new gaps exceeded the ability of the site to refill existing gaps. More importantly, the proportion of area that is taken up by filled gaps increased with distance-to-edge, and this proportion is approximately equal to new gaps in regions further than 80 m from fragment edges (Fig. 5). Also, unlike for new gaps, the effective response of λ for filled gaps was significant, and it penetrated deeply into fragments (Fig. 7). Since regrowth is hampered at edges, then the distri-

bution of existing gaps may still be changing over time in response to the fragmentation.

The distributions of new and filled gaps described here may be affected by the rarity of large tree falls and the relatively brief one-year time span between LiDAR collections. High variation in turnover rates between years has been found in secondary tropical forest in Panama (Yavitt et al. 1995). It is very likely that similar inter-annual variation in gap forming and filling processes exists within our study area. For example, in 2014, Hurricane Iselle made landfall on Hawaii Island, and caused a number of large trees to fall in the study system; these many tree falls created a large number of large gaps—something not seen in the past 6 years of study (*personal observations*). It is possible that tree loss and new gaps creation may be more significantly shaped by fragment edges during rare wind events like this. A longer time span between canopy measurements would certainly capture additional new gaps in the larger size classes, but this would be at the expense of missing the more rapid cycling of the smaller gaps. Therefore, to best characterize both the large and small new gap formation and closure rates of the study area, multiple overflights would be needed.

CONCLUSIONS

After more than a century following fragmen-tation, we found important differences in the gap-phase dynamics of montane tropical forest. Measurable differences were found in the distri-bution of gaps already formed and on the rate of gap closure. Because these differences subsided with increasing distance from fragment edges, smaller fragments should be the most thoroughly transformed. Vaughn et al. (2014) found this to be true for other canopy structure metrics at this site. Because characteristics of the gap size distribution have implications for many process-es taking place under the canopy, this has strong implications for the long-term behavior of forest remnants around the world. Additional long-term studies may provide further insight into how forest canopies change over longer periods of time in response to fragmentation.

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