

Spatial scaling of mountain pine beetle infestations

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Summary

1. The relationship between occupancy and spatial contagion during the spread of eruptive and invasive species demands greater study, as it could lead to improved prediction of ecosystem damage.
2. We applied a recently developed model that links occupancy and its fractal dimension to model the spatial distribution of mountain pine beetle infestations in British Columbia, Canada. We showed that the distribution of infestation was scale-invariant in at least 24 out of 37 years (mostly in epidemic years), and presented some degree of scale-invariance in the rest. There was a general logarithmic relationship between fractal dimension and infestation occupancy. Based on the scale-invariance assumption, we further assessed the interrelationships for several landscape metrics, such as correlation length, maximum cluster size, total edge length and total number of clusters.
3. The scale-invariance assumption allows fitting the above metrics, and provides a framework to establish the scaling relationship between occupancy and spatial contagion.
4. We concluded that scale-invariance dominates the spread of mountain pine beetle. In this context, spatial aggregation can be predicted from occupancy, hence occupancy is the only variable one needs to know in order to predict the spatial distributions of populations. This supports the hypothesis that fractal dispersal kernels may be abundant among outbreaks of pests and invasive species.

Key-words: fractal, infestation outbreaks, mountain pine beetle, scaling, spatial distribution

Introduction

Many invasive species show heterogeneous spatial distributions due to several spreading mechanisms (Ray & Hastings 1996; Williams & Liebhold 2000). Their distributions are often composed of a few large and many nascent small foci, a pattern probably generated by fat or long dispersal kernels (Kenkel & Irwin 1994; With 2004; Marco *et al.* 2007). Pathogen dispersal also exhibits fractal properties that often produce scale-dependent spatial distributions in occupancy (Kenkel & Irwin 1994; Shaw 1995; Despland 2003).

Spatial scale-dependence has been an important assumption for predicting patterns across scales and levels of organization in biology (Brown *et al.* 2002; Haskell, Ritchie & Olf 2002). Typically, many spatial scaling properties assume power-law relationships of the form $Y \propto X^b$, where Y is the variable of interest (e.g. area occupied), X is the measuring scale, and b is a scaling exponent. When this property holds for several orders of magnitude, self-similarity (approximate repetition of patterns with changes in scale) can be assumed. However, heterogeneous distributions are often not self-similar: a diverse combination of occupancy and spatial contagion may result in

occurrence patterns ranging from totally random to clumped (Lennon, Kunin & Hartley 2002; Despland 2003; Gamarra 2005). In some cases, nevertheless, homogeneous fractality in space holds true for a wide range of scales, except when the area occupied is close to the sampled space.

Outbreaks of mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) in British Columbia, Canada, constitute a good example of spatial scaling in ecology. Since 1997, this bark beetle has infested over 7 million ha of lodgepole pine (*Pinus contorta* Dougl.) through pheromone-mediated mass attacks in association with blue fungi (Raffa & Berryman 1983; Safranyik & Wilson 2006). Although endemic, its populations undergo cyclic epidemic events causing large ecological and economic damage (Leuschner & Berck 1985; McCullough, Werner & Neumann 1998). General spatial scaling rules of endemic and epidemic events may inform us of the presence of common, scale- and state-invariant mechanisms for the spread of the beetle.

We hypothesized that occupancy, measured as a proxy for abundance (Williams & Liebhold 2000; He & Gaston 2003), and fractal dimension have a robust scaling relationship; therefore occupancy can be used to predict the spatial heterogeneity of the MPB distributions. Our aims were: (1) to discern whether MPB spatial distributions follow scale-invariant relationships; (2) to derive different spatial scaling metrics (correlation length, maximum cluster size, edge length, number of clusters) from the scale-invariance assumption;

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and (3) to provide a simple, easy-to-measure aggregate variable that links those metrics under a common framework.

A FRACTAL MODEL FOR SPATIAL SCALING

Consider a two-dimensional landscape converted to a grid with dimensional minimum resolution ε . The occupancy, h (area infested by MPB), is expressed as a fraction of whole landscape. Under complete randomness, pixels are occupied following a Poisson distribution. Following Moisy & Jiménez (2004), the mean distance between occupied ε -sized pixels is $r = \varepsilon/\sqrt{h}$. Assuming that $\varepsilon \ll 1$, the probability of finding an occupied box of size w is $1 - e^{-(w/r)^2}$. Thus, we can compute the total number of occupied w -sized boxes as:

$$N(h, w) \propto w^{-2} [1 - e^{-(w/r)^2}] = w^{-2} [1 - e^{-h(w/\varepsilon)^2}].$$

This distribution is scale-dependent, and its fractal dimension, expressed as $D(h, w) = -d \ln[N(h, w)]/d \ln(w)$, is thus:

$$D(h, w) \propto 2 \left[1 - h(w/\varepsilon)^2 \frac{e^{-h(w/\varepsilon)^2}}{1 - e^{-h(w/\varepsilon)^2}} \right]. \quad \text{eqn 1}$$

However, under complete self-similarity, outbreaks follow fractal distributions. Further assuming an infinite two-dimensional space, Gamarra (2005) derived a robust scale-invariant relationship for the fractal dimension:

$$D(h) = 2 - \theta \quad \text{eqn 2}$$

where $\theta = \ln(h)/\ln(\varepsilon)$. Thus, at certain occupancy, we may have a constant, scale-invariant fractal dimension, but this is non-constant among different occupancy values because of its dependence on h . Fractal dimension and occupancy are strongly associated through ε (Latora, Rapisarda & Vinciguerra 1998; Gamarra 2005). This is important because it allows development of a scaling approach to compute several landscape metrics based on non-constant fractal exponents.

Correlation length, ξ_c , measured as the lag distance at which correlations vanish, can be computed from the semivariance equation $\gamma_c \propto \xi_c^{4-2D(h)}$ (Burrough 1983). The semivariogram is usually computed numerically as a weighted variance of the indicator values of the pixels (either 0 or 1) in some neighbourhood of size ξ_c around each pixel. Knowledge of $D(h)$ from equation 2 and a relaxed assumption permits the so-called nugget variance, $\gamma_0 \rightarrow 0$ at $\xi = 0$ due to errors associated with ε (Leduc, Prairie & Bergeron 1994), and thus allows us to avoid numerical computation of the semivariogram. Substituting equation 2 to the semivariance equation and solving for ξ_c leads to:

$$\xi_c \propto e^{\ln(\gamma_c/\gamma_0)/(2\theta)} \propto E \gamma_c^{(2\theta)^{-1}}, \quad \text{eqn 3}$$

where $E \propto \gamma_0^{-(2\theta)^{-1}} \propto \varepsilon^{-1}$ is a normalization factor.

From the dimensional ground, average patch size follows a scaling of the form $m \propto \xi_c^2$, where m is the average patch size (number of pixels of a patch or cluster). Percolation theory

(Stauffer & Aharony 1994) states that, below the percolation threshold, when $h \rightarrow 0$, maximum (M) patch size scales as $M \propto m$; hence $M \propto \xi_c^2$. Thus from equation 3 we derive the scaling relationship:

$$M \propto E^2 \gamma_c^{1/\theta} \propto \varepsilon^{-2} \gamma_c^{1/\theta}. \quad \text{eqn 4}$$

Another landscape metric, the total edge length (number of joins of linear side ε), scales as $L \propto hp(1-p)$, where $p(h, \varepsilon)$ is the average probability that a cell is occupied (Lennon *et al.* 2002; He & Hubbell 2003), and depends on the spatial distribution of the set. However, our self-similarity assumption establishes a direct relationship between spatial correlation and occupancy that can be used to solve for $p(h, \varepsilon)$. As a scale-dependent measure, Allain & Cloitre (1992) defined the lacunarity of a fractal set as $\Lambda(w) = w^{D(h)-2}$, where $w = \xi$ is the scale of interest. Under scale invariance, equation 2 defines $\Lambda(w) = w^{-\theta}$ (Gamarra 2005). This defines the average relative neighbourhood density of a self-similar distribution (*sensu* Ostling, Harte & Green 2000) (Fig. 1a). The average probability of occupancy then becomes $p(h, \varepsilon) = h\Lambda(w)$ (Gamarra 2005) (Fig. 1b). Assuming a binomial distribution within window boxes of size ξ_c , the scaling of edge length against occupancy is:

$$L \propto h^2 \Lambda(\xi_c) [1 - h\Lambda(\xi_c)] \propto h^2 \xi_c^{-\theta} (1 - h\xi_c^{-\theta}) \propto h^2 \xi_c^{-\theta} \exp(-h\xi_c^{-\theta}) \quad \text{eqn 5}$$

Finally, the number of patches can be computed using $N \propto p^m(1-p)^l$ (Stauffer & Aharony 1994; He & Hubbell 2003). Typically, an occupancy percolation threshold is achieved at h_c where the number of patches reaches a maximum. In landscape ecology and percolation theory, this threshold can cause sudden transitions in many properties of the system. The number of joins on the perimeter of the average patch is $t = m\mu \forall h \leq h_c$. Percolation theory defines the percolation threshold from the number of patches as $h_c = (1 + \mu)^{-1}$. Here μ is a proportionality constant between m and t . Introducing again the lacunarity-based definition of p , when $h \ll 1$, the equation can be approximated as:

$$N \propto h \xi_c^{m\theta} (1 - \xi_c^{-\theta})^{m\mu} \propto h \xi_c^{m\theta} \exp(-m\mu \xi_c^{-\theta}). \quad \text{eqn 6}$$

Methods

We extracted patterns of occupancy in MPB populations in British Columbia from publicly available data (<http://cfs.nrcan.gc.ca/subsite/mpb>) providing images that we converted to lattices of 3×3 -km resolution. The 1964–2002 infestation maps (with data lacking in 1997 and 1998) were produced by manual transcription of damaged zones observed from aerial surveys by the Canadian Forest Service, Natural Resources Canada and the British Columbia Ministry of Forests.

To infer scaling using a fractal approach, one first needs to check whether the assumption of fractality is general and plausible. Hence we tested whether cluster size distributions of damaged areas followed power-law scaling. We fitted cluster size distributions using the `glnm` R package from J. Lindsey (<http://popgen.unimaas.nl/~jlindsey/rcode.html>). The goodness of fit of the zeta (power-law) model was tested using Kolmogorov–Smirnov tests.

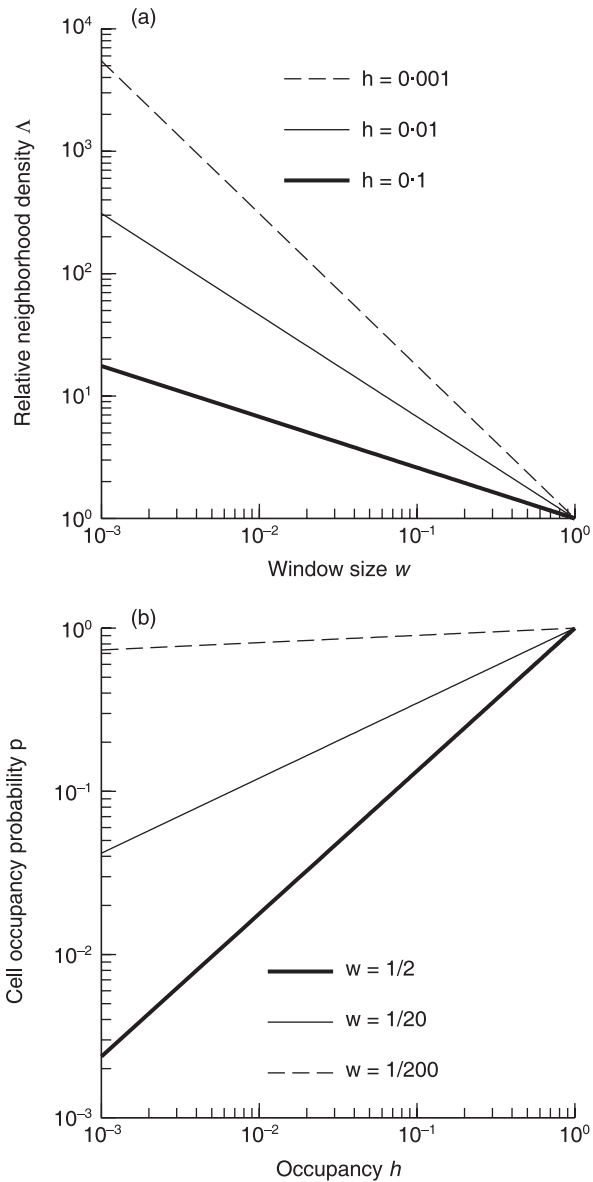


Fig. 1. Theoretical scaling probabilities under scale-invariant distributions. (a) Power-law decay in relative neighbourhood density (lacunarity) with regard to window sampling size for different values of occupancy. (b) Probability of cell occupancy increases with occupancy under different window sampling sizes. In all cases, $\epsilon = 1/256$.

To test the validity of the scaling relationships (equations 2–6), we computed the landscape metrics used in those derivations. Fractal dimension was computed via the box-counting algorithm with successive window sizes ranging from 6×6 to 220×220 pixels by intervals of 2. Indicator semivariograms allowed computation of correlation lengths through qualitative detection of sills. Cluster-related measurements such as size, total edge or number of patches (clusters) were computed with Moore conditions, which define clusters by neighbourhood pixels connected by edges or vertices. When no neighbours were present, a single patch was counted as an individual cluster. We used an iterative Levenberg–Marquardt least-squares minimization algorithm (Press *et al.* 1992) to fit the nonlinear scaling models, and computed the corresponding exponents via Kolmogorov–Smirnov goodness-of-fit tests after discarding the largest clusters in the distributions (Fig. 2).

Results

The number of occupied cells from 1964 to 2002 indicates the existence of 1.5 epidemic cycles with peaks in 1985 and 2002 (Fig. 2). Metapopulations grew more quickly in the second peak, probably due to higher climatic suitability and milder climate conditions (Carroll *et al.* 2004).

We found power-law distributions of cluster sizes in 24 of the 37 years. The other 13 years mostly correspond to years in endemic states (low occupancy levels; Fig. 2). Although statistically not significant, all years except those two with lowest occupancy presented power-law decay across a substantial part of the cluster size spectrum. Power laws following cluster size distribution $p(s) \propto s^{-(\alpha+1)}$, where α is the exponent of a cumulative distribution $F(S > s) \propto s^{-\alpha}$, applied to those years when outbreaks were most significant, and also applied to about half of the endemic years between the two epidemic peaks. For the peak years, the exponent from the cumulative distribution $\alpha \approx 1.09$ provided a hyperbolic-squared decay in cluster sizes for the probability density function. Although wildly different in terms of occupancy, MPB maps for 1985, 1986 and 1988 follow the same scale-invariant cluster size distribution (Fig. 3). The 1987 map does not have power-law decay over the whole spectrum of cluster sizes, and also presents localized big clusters.

The spatial distributions of outbreaks of MPB strongly supported our predictions. The fractal dimensions of MPB

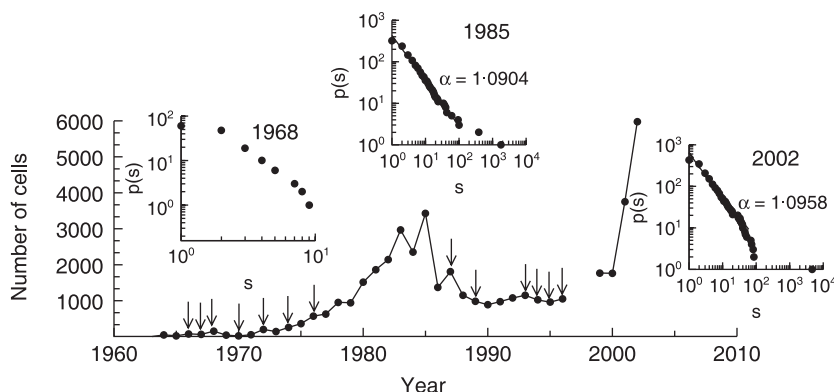


Fig. 2. 1963–2002 series for the number of 3×3 -km cells with presence of mountain pine beetle infestations. Arrows indicate years in which the cluster size distributions do not follow a power-law decay. Insets are cumulative distributions best fitted from their respective probability density functions: 1968, non-zeta; 1985, zeta $z(\alpha + 1)$; 2002, zeta $z(\alpha + 1)$. The exponent for the power-law distribution is included.

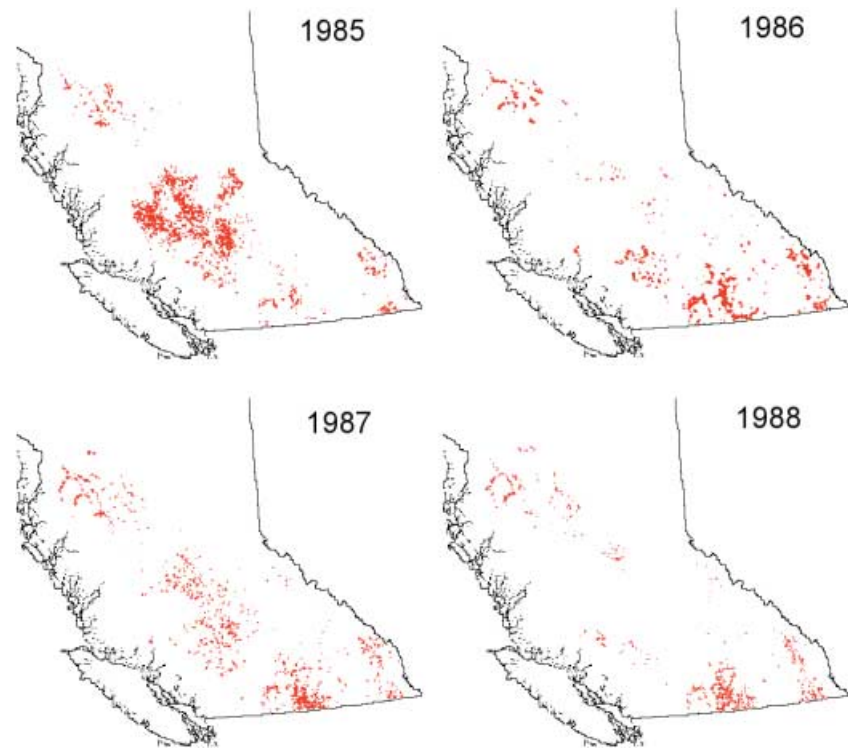


Fig. 3. Maps of the 1985–88 mountain pine beetle outbreaks in southern British Columbia, Canada. 1987 is the only year not described by a power-law cluster size distribution.

distributions agree with equation 2, as opposed to the pattern followed under the Poisson distribution given by equation 1 (Fig. 4). The very large embedding landscapes ensured that occupancy was low enough so that finite-size effects did not complicate analysis. Because equation 2 is based on scale-invariance assumptions, we could assume homogeneous fractality in the range of occupancies of the MPB data. Average correlation lengths agree with equation 3 in Fig. 5(a). A maximum correlation length of 120 km appears in 2002 (the largest infestation year). Equation 4 also agrees with the data. Although our fractality assumption overestimates maximum cluster size in those non-power-law years (Fig. 5a), the aggregated scaling relationship still holds.

Edge length and number of clusters also scaled according to our models (equations 5 and 6, respectively). The number of clusters follows a humped curve tending to some maximum, although it has a concavity stronger than that predicted by a model based on the negative binomial distribution (He & Hubbell 2003; Fig. 5(b)). Furthermore, the percolation thresholds in both models show some disagreement. In the negative binomial model, $h_c \approx 0.021$, while our model shows $h_c \approx 0.031$. This is due to the fact that our model can incorporate more aggregated distributions, so that a larger occupancy is needed to achieve full connectance of the landscape.

Discussion

We have provided an explicit model (equation 2) for the scaling relationship between occupancy and fractal dimension that assumes homogeneous fractality under some range of

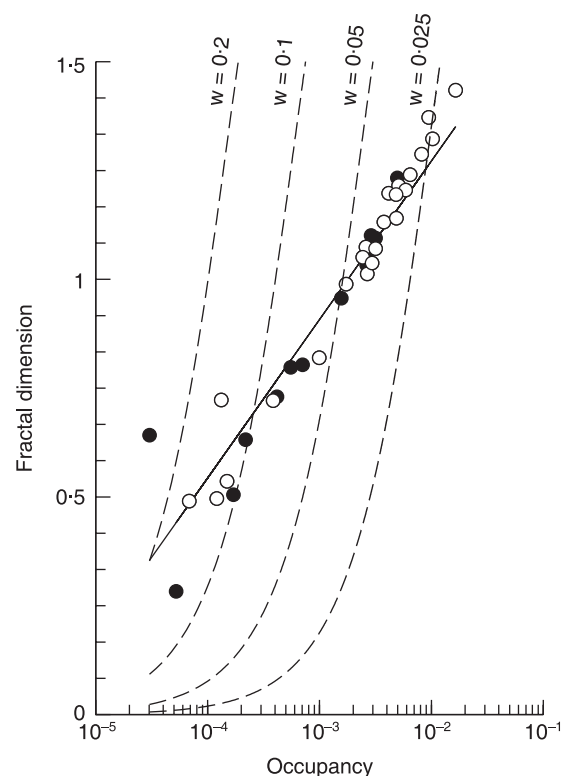


Fig. 4. Fractal dimension–occupancy plot. White and black circles depict years with power-law- and non-power-law-distributed cluster sizes, respectively. Dashed and solid lines correspond to the scale-dependent equation 1 and the scale-invariant equation 2, respectively.

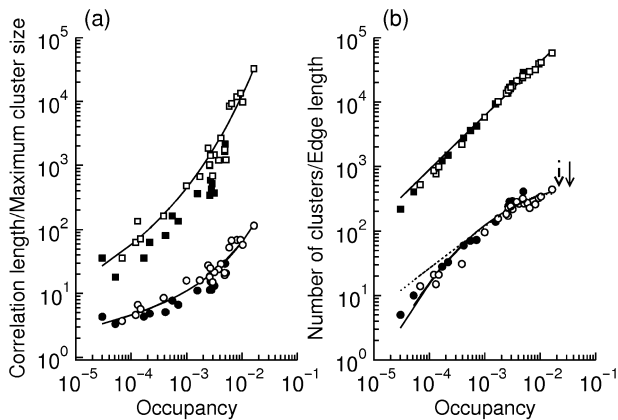


Fig. 5. Relationships of landscape metrics derived from the scale-invariant relationship in equation 2. White and black symbols are as in Fig. 4. (a) Correlation length (circles, km) and maximum cluster size (squares, cell number) and respective fits of equations 3 and 4. (b) Number of clusters (circles) and total edge length (squares, in number of joins). Solid lines: respective fits of equations 5 and 6. Dashed line: negative binomial model fit. Percolation thresholds for the fractal and the null model are shown by solid and dashed arrows, respectively.

occupancy. This contrasts with the Poisson-based scale-dependent model (equation 1). We have derived five different landscape metrics based on scale-invariance: correlation length, maximum cluster size, average cluster size (not shown in figures), total edge length, and number of clusters. However, other spatial metrics could be derived based on percolation theory.

Rather than following constant scaling exponents, our models (equations 3–6) provide some concavity in log–log curves, more visible in the number of clusters (equation 6; Fig. 5b). This concavity is due to the change in fractal dimension with occupancy. However, finite size effects may strongly upset this relationship: the use of constant exponents in the absence of characteristic length scales is not feasible in real systems, due to the intrinsic finiteness of any space (Lennon *et al.* 2002; Halley *et al.* 2004; Šizling & Storch 2004). To avoid this limitation, other alternatives have been proposed: use of non-constant exponents (multifractals) or exponent-dependent normalization factors (scale-dependent lacunarity, with specific cases like exponential cut-offs). In order to predict the spatial scaling properties over the whole range of possible occupancy values, we would need an explicit formulation for the fractal dimension–occupancy relationship accounting for the constraints imposed by a finite space, such as the likely acceleration in the fractal dimension once the percolation threshold has been reached.

Percolating states can provide qualitative information on the temporal dynamics of the system. When occupancy is close to percolate, we could predict the imminent arrival of a maximum peak in the global beetle outbreak using equation 6. This is the case for 2002, the year closest to the percolation threshold derived from equation 6, where the infestation approaches a state where the resource is about to be depleted.

The fact that years not described by power-law distributions tend to follow the scale-invariant relationship may constitute

a paradox. However, this pattern is probably due to sampling resolution, producing the following effects.

1. Undercounts – at the smaller spatial scales, there is an undercount of cell occupancy (e.g. cluster size distributions for 1968, 1985 and 2002 in Fig. 2) that may be the result of the intrinsic difficulties in spotting small infestations from aerial surveys, more so if trees are below the canopy and in a non-outbreak year.
2. Coalescence – at larger spatial scales, cluster size distributions bend upwards due to coalescence of clusters into bigger clusters (avoidable with better resolutions) (e.g. 1985 and 2002 insets in Fig. 2).
3. Non-homogenous resource landscapes, which imply the presence of unsuitable areas between clusters: for larger clusters, some distributions tend to bend downwards due to the absence of pine habitat between clusters (e.g. 1968 and 2002 insets in Fig. 2).

Nonetheless, power-law scaling over a substantial section of the cluster size distribution in all years except two (see e.g. inset in Fig. 2 for 1968) is consistent and ensures the robustness of equation 2 across our data.

Two consequences arise for MPB spread and dynamics. First, all epidemic and many of the endemic states follow fractal cluster size distributions that result in the fractal dimension–occupancy scaling equation 2. This is a significant step, in that derivation of aggregate spatial properties simply from occupancy allows us to develop spatially implicit models for distributions: colonization parameters can incorporate aggregate, occupancy-dependent spatial properties derived from such scaling relationships (such as metapopulation capacity or lacunarity, *sensu* Gamarra 2005). Hence there may be no need to develop dynamic equations for both occupancy and spatial aggregation, because they are tightly linked. Furthermore, the fractal dimension–occupancy relationship provides clues on the build-up of epidemic clusters growing towards percolating structures. This supports the importance of fat-tailed dispersal or fractal kernels in the colonization and extinction of outbreak insects (Kenkel & Irwin 1994; Shirtcliffe, Kenkel & Entz 2002), due to this tight scaling relationship.

Second, robust landscape metric–occupancy relationships allow the prediction of spatial indices (five of them derived here: fractal dimension, maximum patch size, edge length, number of patches and correlation length) from the sole information of occupancy. Some measures, such as average correlation length or maximum cluster size, are useful in characterizing distributions, and may provide information about spatial spread and potential forest-management actions. For example, correlation length may indicate the average size of continuous damaged forest, while maximum cluster size may represent the potential extent of maximum continuous damage.

Many studies have focused on the effect of resource quantity and distribution on the dynamics and distribution of consumer populations (Williams & Liebhold 2000; Gamarra 2005; Økland *et al.* 2005). However, long-distance dispersal diminishes the role of resource distribution by increasing the connectivity between patches of resources (With 2004). Hence, contrary to consumer–resource-based assumptions, it is not obvious that

the distribution of lodgepole pine forest in British Columbia may be playing such a constraining regulatory effect in the spread of MPB.

Some other real systems and simulation experiments show patterns that follow our derivations qualitatively. Despland (2003) showed that areas damaged by locust populations follow a scaling relationship similar to equation 2. Data on breeding birds and butterflies in Holland (Olf & Ritchie 2002), forest habitat for the Florida panther (Kerckhoff, Milne & Maehr 2000), and simulations of disturbance regimes in artificial landscapes (Hargis, Bissonette & David 1998) also support equations 2 and 5. These patterns pervade even in invasive species with high growth rates and a lack of natural enemies, where long-distance dispersal is followed by local reproduction in the area surrounding the founder parent (Marco *et al.* 2007). The apparently widespread nature of the relationship between fractal dimension and occupancy points to the presence of general mechanisms for the spread and distribution of many living organisms. By studying these patterns in other pests, invasive and pathogenic species, we will be able to assess the generality of the role played by habitat connectivity. The potential of such robust relationships includes their use in risk analysis, pest control and the design of protected area networks. However, forecasts of population outbreaks will be feasible only under adequate modelling frameworks for the dynamics of those populations.

The robustness of the model would also improve population monitoring. Although regular surveys across large, susceptible landscapes are to be recommended, fractal scaling suggests that the spatial distribution of sampling effort should not be uniform. Rather, special attention should be paid to managing areas that are susceptible to incipient large local outbreaks, while the prompt localization of small endemic bursts demands that rigorous sampling be realized in other areas at longer distances than expected if short-term, diffusion-like dispersal is assumed.

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