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Determining the size of a complete disturbance landscape: multi-scale, continental analysis of forest change

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Abstract The scale of investigation for disturbance-influenced processes plays a critical role in theoretical assumptions about stability, variance, and equilibrium, as well as conservation reserve and long-term monitoring program design. Critical consideration of scale is required for robust planning designs, especially when anticipating future disturbances whose exact locations are unknown. This research quantified disturbance proportion and pattern (as contagion) at multiple scales across North America. This pattern of scale-associated variability can guide selection of study and management extents, for example, to minimize variance (measured as standard deviation) between any landscapes within an ecoregion. We identified the proportion and pattern of forest disturbance (30 m grain size) across multiple landscape extents up to 180 km^2. We explored the variance in proportion of disturbed area and the pattern of that disturbance between landscapes (within an ecoregion) as a function of the landscape extent. In many ecoregions, variance between landscapes within an ecoregion was minimal at broad landscape extents (low standard deviation). Gap-dominated regions showed the least variance, while fire-dominated showed the largest. Intensively managed ecoregions displayed unique patterns. A majority of the ecoregions showed low variance between landscapes at some scale, indicating an appropriate extent for incorporating natural regimes and unknown future disturbances was identified. The quantification of the scales of disturbance at the ecoregion level provides guidance for individuals interested in anticipating future disturbances which will occur in unknown spatial locations. Information on the extents required to incorporate disturbance patterns into planning is crucial for that process.

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Introduction

Disturbances are integral components of ecosystems (Pickett and White 1985, Turner 1989); therefore, research and management need to incorporate considerations of disturbance into planning processes and study design. The typical size and pattern of disturbance

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events is critical for understanding their effects on ecological and human systems, as well as predicting long-term effects. (Turner et al. 1993, Zurlini et al. 2007). Landscape extents and their relationship to the size and pattern of disturbances in those landscapes play an important role in theoretical assumptions, acknowledged or not, about landscape stability, variance, and equilibrium (Turner et al. 1993). However, because most disturbances are relatively infrequent compared to the time period over which researchers have spatial data (e.g., the satellite record), and often cover large spatial extents, identifying the necessary spatial scale to either incorporate the effects of historical disturbances or accommodate future disturbances and remain representative of a given region is challenging. Therefore, quantifying disturbance pattern, size, and scale is required as part of building a robust study or management design.

Researchers, policy makers, conservationists, and resource managers all need to know the typical scale of a disturbance for a given area of interest (Mayer et al. 2016). Why is this important? As an example, consider conservation reserve design for a given ecosystem type or ecoregion, where optimal landscape extent is often one where natural disturbance regimes can affect the landscape unhindered by active management in relatively intact landscapes such as wilderness areas or some boreal forest regions. This is sometimes considered the requisite extent for conservation, a scale broad enough to encompass and be representative of natural system dynamics. Reserves where the landscape:disturbance extent ratio is generally high would be generally be expected to be relatively stable to disturbances (though with some amount of temporal variability; Turner et al. 1993). In this case, stable implies that despite any given disturbance event, the relative amount of habitat remains generally consistent (at a scale relevant to the process being protected). However, though incorporating natural disturbance dynamics into reserve designs is a critical need (e.g., Leroux et al. 2007, Leroux and Rayfield 2014), most protected areas are not at the necessary scale and thus may be ineffective at ensuring long-term persistence of biodiversity and ecological processes (Cabeza and Moilanen 2001, Bengtsson et al. 2015, Pressey et al. 2007). In places where conserving a landscape large enough for unhindered persistence of the typical disturbance regime is not practical, knowledge of the historical range of variability in space and time is required for management of an artificial disturbance regime within conserved areas (Baker 1992, Bissonette 2012). These requisite pieces of information—typical disturbance size and patterning—therefore have important implications for study design and conservation planning (Turner 2010, Betts et al. 2010, Wiens 2009, Mayer et al. 2016).

An understanding of typical disturbance-landscape scale relationships is important for experimental design and efficiency as well. It would be useful to know, for example, if a landscape of 400 km^2 is typically large enough to encompass the natural range of variability in disturbances found in boreal forests, or 10 km^2 is enough for eastern hardwoods. One might expect that the coastal maritime forests, dominated by a fine-scale gap disturbance regime, might be represented by a smaller landscape extent than southern Rocky Mountain montane forests, as fine-grained disturbance events are spread throughout the region (gap dynamics driven by wind, with small mean size, Ott and Juday 2002), in contrast to larger fire events in the Rocky Mountains. This information is needed to determine "how big is big enough" when designing disturbance distribution research and looking for changes in baseline disturbance characteristics (e.g., Buma and Barrett 2015).

In addition to disturbed area, the spatial pattern of disturbance events is an important aspect of ecoregion or biome-level disturbance regimes, and individual disturbance drivers generally have characteristic patterning (Turner et al. 1997). There are a variety of metrics relevant to disturbance patch shape (for examples, McGarigal et al. 2012) and similar to area, understanding how disturbance patterns scale across landscapes is important for study and reserve designs. Variance across scales reveals something about the variability in the processes driving disturbances. Low variance implies low spatial variability in both the drivers of the disturbance and any stochastic factors initiating disturbance events. In contrast, areas with high spatial variance in either the drivers of disturbance events (e.g., hurricanes) or stochastic initiation factors (e.g., lightning strikes) would presumably have higher variance in spatial disturbance processes across the landscape.

This study quantifies how variance changes with landscape extent within biomes and ecoregions (smaller sub-portions of biomes defined to be relatively homogenous in terms of species composition and functioning; Loveland and Merchant 2004) across the North American continent, focusing on forest disturbances at the ecoregion scale. Ecoregions are relatively homogenous ecological areas defined using a variety of metrics, most commonly dominant plant type and climate. Thus, they are useful aggregational tools for spatially scaling to broader regions (Loveland and Merchant 2004, Omernik and Griffith 2014) and because policy decisions, management (Omernik and Griffith 2014) as well as ecological research (e.g., carbon balance, Turner et al. 2015; land use change, Sayler et al. 2016) are often carried out at the ecoregional level. Finally, because disturbances and ecosystem structure and functioning are tightly linked, ecoregions also incorporate (implicitly or explicitly) disturbance regimes.

Randomly selected small landscapes, those with a relatively limited spatial extent, are expected to have high variability in their disturbance characteristics relative to the "actual mean" of the ecoregion; in other words, small landscapes are less likely to be representative of the actual disturbance characteristics of the ecoregion they represent (for the time period of observation), simply because at small extents, single disturbance events can completely cover or miss a small landscape. As extent of any random landscape increases, however, the area should become more reflective of the actual ecoregion disturbance characteristics as more area (and more or complete events) are encompassed, and theoretically, variability between random landscapes within an ecoregion should decrease as landscape extent approaches the ecoregion extent (Fig. 1). This variance-scale relationship is important to quantify, because it informs theoretical expectations about relative stability for any given landscape extent

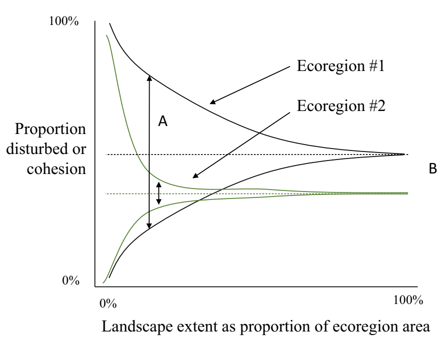

Fig. 1 Variance in disturbance metrics as a function of landscape extent within an ecoregion. At relatively small landscape extents relative to the ecoregion, there is a wide range (A) in observed metric values compared to the "true" ecoregion proportion disturbed (B). Theoretically, as the landscape extent approaches the complete extent of the ecoregion, that variance goes to zero (convergent lines). Different ecoregions may have different mean proportion disturbed values and variance across scales

(Turner et al. 1993, Wimberly et al. 2000), important for research, and planning purposes (though the temporal scale of observation, often relatively short compared to disturbance return intervals, also introduces variance, see "Discussion"). Yet, this quantification has not been done in a comprehensive, empirical fashion due to a lack of disturbance data at the requisite grain and extent.

The purpose of this descriptive study was to quantify the proportion and pattern of disturbance for the ecoregions of North America (Olson et al. 2001) at multiple scales. This information is intended to be a reference and a baseline for local researchers and land managers who are interested in incorporating a quantitative, scale-based perspective on disturbances in ecological research or land management, for example, determining landscape sizes that minimize expected variability caused by future disturbances. In addition, quantification of these patterns as actually observed will be a useful way to test emerging, broad-scale modeling efforts which incorporate multiple disturbance types and fine grains. Data for all ecoregions at all spatial scales is included in the supplementary documentation; illustrative results are presented below.

In this study, each ecoregion was analyzed for mean proportion disturbed and contagion (clumping) for a range of landscape extents (from 0.0081 to 179.8 km^2). This was done for two different perspectives: the ecoregion level, where the analysis focuses on all pixels, and the "class" level, where all landscapes analyzed were centered on a disturbed pixel (the disturbed class). The ecoregion level is useful for estimating general attributes of those systems, e.g., proportion disturbed. Despite the fact that multiple disturbances, operating at characteristic spatial and temporal scales, occur in the same ecoregion, this level of aggregation has proven useful in estimating the effects of multiple disturbance types on ecosystem functioning (Turner et al. 2015, Sayler et al. 2016). The class perspective focuses on disturbed pixels only and is useful for exploring attributes of the disturbances themselves, e.g., are they typically highly clumped and are those clumps isolated?

The purpose of this study is to generate a useful, quantitative dataset for researchers and managers interested in the relationship between disturbance patterns and landscape scale. This dataset should be useful to designing management, research, or conservation plans which need to accommodate uncertainty in the specific location of future disturbance events by determining what extents are required to encompass the natural range of variability in disturbances for any given ecoregion. For two spatial disturbance characteristics, percent disturbed and contagion of the disturbance, we ask the following:

1. How does mean proportion disturbed vary as a function of landscape extent at both the ecoregion and class levels?
2. How does the spatial arrangement of disturbances change as a function of landscape extent at both the ecoregion and class levels?
3. What is the minimum landscape extent required to minimize variance among landscapes (within an ecoregion)? In other words, how large does a landscape need to be to represent the ecoregion in terms of proportion disturbed and contagion?

Methods

Metrics

Percent disturbed was defined as the proportion of the landscape that was disturbed, ignoring missing data. On a raster map of disturbance, percent disturbed is derived by counting the number of disturbed pixels in a landscape divided by the total area of the landscape. *Contagion* was defined as the conditional probability that a disturbed location in the landscape was adjacent (using the 4-neighbor rule) to another disturbed location (Riitters et al. 2000). This is one way to describe the shape of a disturbance, as more "clumpy" or compact disturbances will have a larger contagion value and more dispersed, single-pixel disturbances a lower value assuming the same total proportion disturbed. Contagion ranges from zero for a checkerboard pattern to 100 for a pattern of maximum compactness and has a higher value when disturbances are in larger patches and a smaller value when the more disturbances are isolated or occur in smaller patches. Contagion is calculated from the attribute adjacency table which describes the co-occurrence of adjacent pixel pairs; of the total number of adjacent pixel pairs that include at least one disturbed pixel, contagion is the proportion for which both pixels are disturbed. Note, this is not identical to other measures of contagion (also based off the attribute adjacency table) such as in O'Neill et al. (1989). If a landscape had zero disturbance, contagion was assigned a zero value. The two metrics were chosen because they represent two different descriptors of the disturbance regime of an ecoregion and across scales: proportion disturbed is related to the extent of disturbances within a given extent of land and contagion is related to the general shape of disturbances within that extent.

Input data

A global map of forest cover disturbance from 2000 to 2012 (Hansen et al. 2013) was used for the multiscale analysis of disturbance amount and contagion. This dataset identifies pixels which saw a loss of tree cover within the study period and was derived from MODIS and Landsat imagery. Because the dataset provides information on forest cover and disturbance in a comprehensive (wall-to-wall) fashion at a fine spatial resolution, it is useful for disturbance analysis at continental scale. Following procedures described by Riitters et al. (2015), the North American portion of the global map of tree cover disturbance was converted to an equal-area projection with a spatial resolution of 900 m^2 (to match the 30×30 m nominal resolution of the Landsat images). The percent disturbed area and contagion were then measured at 10 observation scales defined by landscape extents (square) equal to 0.0081, 0.0225, 0.0441, .0729, .1521, .6561, 2.7225, 11.0889, 44.7561, and 179.828 km^2. By using a moving window algorithm (Riitters et al. 1997) to make the measurements, the results of the measurements were mapped at the original 30 m resolution of the tree cover disturbance map and covered North America. The pixel value on one of the 20 resulting maps represents either the proportion of forest disturbed or contagion within the landscape extent centered on that pixel, at one of the 10 different landscape extents (10 scales $\times$ 2 metrics). Note that disturbed/undisturbed is not necessarily a binary distinction and some low-intensity disturbances may be missed by this product. Because this study strictly focuses on forest disturbances, non-forested pixels are considered undisturbed in the analysis of proportion disturbed, and they contribute (by definition) no information about disturbance contagion. This was done for all pixels in North America. This wall-to-wall processing design, where each pixel was processed at each spatial scale, enabled evaluation of disturbance shape (the contagion metric) and the multiple scale method at a single point is analogous to using a semivariogram-like spatial statistical methodology.

Sampling design

A systematic sample of two million locations was then extracted from the "stack" of 20 maps of disturbance amount and contagion, along with the identity of the ecoregion (Olson et al. 2001) which contained each location. Primarily non-forested ecoregions were retained for analysis for completeness and because it is difficult to derive a threshold (for example, in terms of percent of the ecoregion covered) of forested vs. non-forested across all regions, though the results are potentially less relevant to management in those ecoregions (e.g., prairie-type regions). Locations with missing data (e.g., ocean and inland water bodies identified by Hansen et al. 2013) were excluded from the analysis, giving a final dataset of 1,128,765 points. At this sampling density (approximately one point per 22.5 km2), there is fractional overlap at the two largest landscape extents (44.8 and 179.8 km^2). This is a consequence of dense sampling and large investigative landscape sizes. The lack of complete independence at these extents is not a concern for two reasons. First, because a moving window operates one pixel at a time, it is entirely appropriate for there to be autocorrelation in the resultant maps, and correlative patterns picked up by larger or smaller windows represent frequency patterns in the underlying data, namely, lower or higher frequency patterns, respectively. Second, ecoregions are not being compared statistically to other samples, it is not as problematic. To confirm, a second analysis was conducted at 1/10th the sampling density (data not shown). The observed scale-patterns were the same as at the full sampling density, though several small ecoregions were not sampled (and sample sizes in many ecoregions were quite small). Therefore, results are presented for the entire two million sample point density.

At each sampling point, the proportion disturbed and contagion were quantified for each of the landscape scales and the ecoregion recorded. This gives a "stack" of values for each point, quantifying the proportion disturbed in a 0.0081 km^2 landscape around that point, a 0.0225 km^2 landscape around that point, etc. While any single point within an ecoregion may be affected by a disturbance, theoretically, the mean proportion disturbed and contagion values should approach the "true" ecoregion values (and the standard deviations between landscapes in that region should approach 0) as the size of the landscape extent approaches the size of that ecoregion (Fig. 1). This was assessed for both the ecoregion level and the class level. At each spatial scale, the mean and standard deviation over all the sampled landscapes (in a given ecoregion) were calculated and converted to percent value, such as 10% disturbed.

For the ecoregion scale, all sampled locations within the ecoregion were used and results are presented relative to the mean and standard deviation of landscapes across scales. A secondary analysis comparing sampling extent and number of samples to estimated proportion disturbed is also presented. This is useful in determining the necessary number of landscapes required to adequately estimate overall ecoregion disturbance levels.

For the class level, only sample locations that were themselves disturbed were retained. This represents studies focusing on disturbed areas and changes the focus from study landscapes effectively sampled at random (without regard to disturbances) to landscapes centered on a disturbed patch. A secondary analysis relating the ratio of proportion disturbed to contagion across scales is also presented, which is useful in determining the average size of a disturbance event and the extents required to describe it within a landscape. It is intended to unite the two metrics into a single, cross-scale descriptor which can be used to compare disturbance-scale characteristics across biomes.

Minimum extent

The allowable amount of variance between landscapes within an ecoregion, which is analogous to the amount of uncertainty in terms of disturbance amounts for study design/reserve planning, will vary depending on application. Here we arbitrarily chose a standard deviation between landscapes < 10% as the cutoff for "minimizing variance." However, all values at all scales are reported in the supplementary data so that readers may evaluate any potential scale relative to the landscape variance in their ecoregion of interest.

All spatial extractions and statistical analyses were conducted in R (R Core Team, 2015) using the raster package (Hijmans and van Etten 2015).

Results

The supplementary data table contains all the ecoregions with statistical summaries of mean, median, maximum, minimum, range, kurtosis, skew, and standard error for both percent disturbed and contagion, and for all study area sizes at both the ecoregion and class levels (for example, see Table 1). Those data are the basis for the following figures and should be used when looking at any individual study area (if not presented in the text).

The following generally reports on two broad regions with contrasting disturbance regimes, the coastal wet forests of northwest North America (typically wind triggered gap-scale dynamics, but with a strong logging presence in the southern ecoregions) and interior boreal forests (typically large fires, unmanaged) for illustrative purposes. For general location, see Fig. 2. For exact location of each individual ecoregion, see Olson et al. (2001).

Proportion disturbed (mean)

At the ecoregion level, proportion disturbed is not a function of the scale of analysis assuming an adequate sample size that suitably samples the entire landscape. This sample size does vary as a function of landscape scale, however (Fig. 2). Standard error declines with an increasing landscape extent and sample size. Ecoregions with larger and more punctuated disturbance regimes (boreal forests) tended to require a larger sample size at all scales. At the class level, estimates of proportion disturbed do vary as a function of landscape extent (Fig. S1). Ecoregions with generally larger disturbances had a larger proportion disturbed even at broad landscape extents, and regions with lower proportion forested had correspondingly lower proportion disturbed.

Proportion disturbed (standard deviation)

Variance between sample landscapes decreased as the extent increased for nearly all ecoregions, with the highest variance generally found at the smallest landscape sizes (Fig. 3). In other words, there was relatively high variability between locations when looking at small extents, as expected. The largest extents sampled did reduce variability between landscapes substantially for many ecoregions, though it varied as a function of typical disturbance regime. The ecoregions associated with the Interior Taiga biome showed relatively high variance in percent disturbed even at the largest landscape sizes, though there was a large range—the interior Alaska-Yukon lowland ecoregion had high variance, while the southern Hudson Bay taiga had somewhat lower, approaching 5% variance at the largest window sizes. Pacific coastal forests were highly variable, from a high in the south (coastal Pacific and Willamette valley forests; heavily managed for timber production, mixed disturbance regime including fire) to low values in the north (Northern Pacific Coastal forests and the Queen Charlotte Islands; very little anthropogenic presence, small-gap disturbance regime primarily driven by wind, no fire).

Similar patterns were seen at the class level analysis, though the values were considerably higher (Fig. S2). Because class-scale values are centered on disturbance events, both the boreal and the coastal forests generally had similar variance in proportion disturbed at small

Table 1 Excerpt of summary statistics as a function of scale for the Interior Yukon dry forest ecoregion. Values come from 3625 “landscapes” of differing extents within the ecoregion and express mean and variance distributional statistics for both proportion disturbed and contagion metrics. The complete table includes these values for all ecoregions and extents, and further includes minimum, maximum, and median values

Metric	Landscape size (km^2)	Mean	Standard deviation	Range	Skew	Kurtosis	Standard error
Proportion disturbed	0.0081	2.70	15.01	99.61	5.73	31.80	0.25
	0.0225	2.66	14.41	99.61	5.75	32.44	0.24
	44.7561	2.60	10.38	87.06	4.98	26.45	0.17
	179.828	2.55	8.20	70.98	4.27	20.15	0.14
Contagion	0.0081	2.49	14.36	99.61	5.96	34.89	0.24
	0.0225	2.69	14.44	99.61	5.62	31.02	0.24
	44.7561	18.02	24.20	93.73	1.77	1.95	0.40
	179.828	28.52	27.64	90.59	1.00	−0.51	0.46

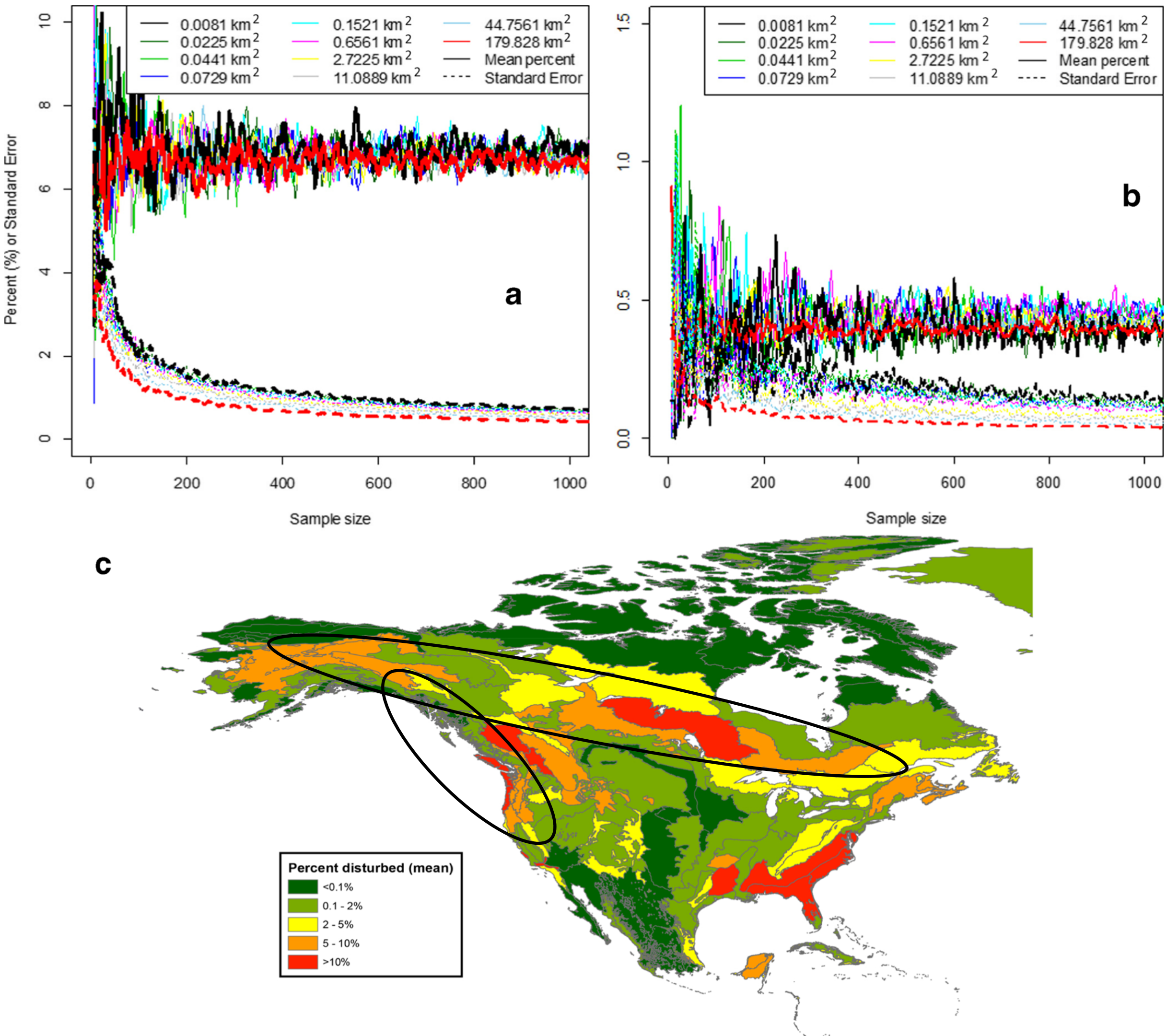

Fig. 2 Effects of changing landscape extent on estimated percent of forest disturbed across the landscape and standard error of that estimate. Larger samples approach the true mean more quickly, with lower standard error throughout. **a** Interior Alaska-Yukon lowland taiga ecoregion. **b** North Pacific coastal temperate rainforests ecoregion. Note differing scales. **c** Ecoregion disturbed percentages (forested area; cumulative 2000–2012). Ovals denote general location of ecoregions used for illustrative purposes in Figs. 3, 4, 5, 6, 7

extents but the coastal forest variance dropped rapidly as landscape extent increased, whereas the variance in the boreal forests stayed generally high.

Contagion (mean)

Contagion increased as window size increased across the ecoregions (Fig. 4), suggesting that larger window sizes are likely to include a rare, large event. Because contagion results from the ratio between interior and exterior events, it is not scaled to landscape extent in the same way percent disturbed is (disturbed area/landscape extent), thus large events (if seen in the landscape) increase the contagion score independent of landscape extent. Smaller windows are likely to be dominated by small, background disturbance events (high perimeter to area ratio), so these rare events would have a large influence on this shape metric and are more likely to be observed with a larger landscape extent. Surprisingly, boreal forests had lower mean contagion

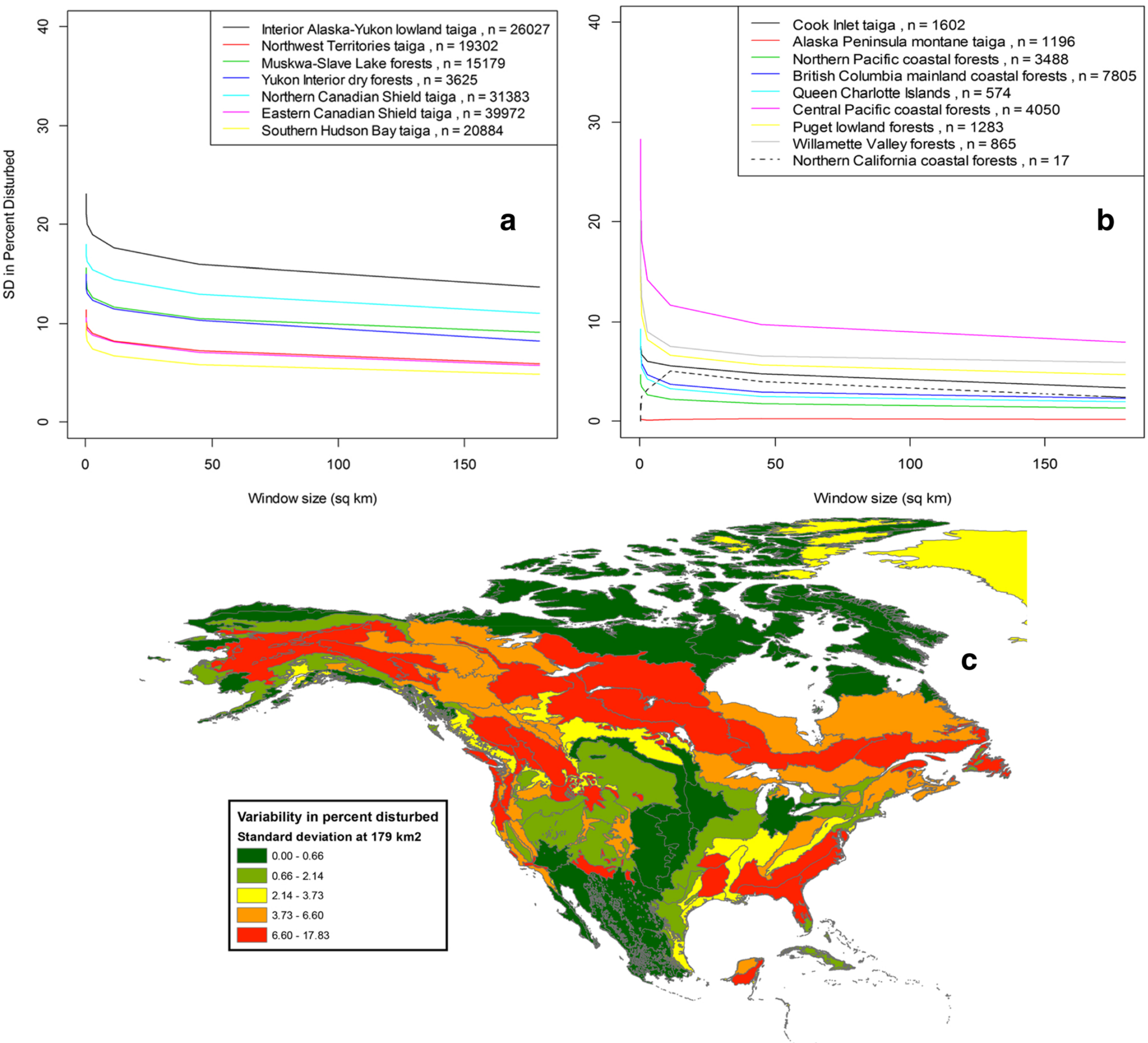

Fig. 3 Ecoregion-scale standard deviation between samples as a function of landscape extent. Variability between small landscapes is generally high, but drops off considerably at extent increases and differences between landscapes decrease. **a** Interior, fire dominated taiga biomes. **b** Coastal, wind/gap dominated biomes. **c** Map of standard deviation between landscapes at the ecoregion level for the continent. Values for the graphed landscapes above match their respective values on the map at the 179 km^2 extent

than coastal forests at the ecoregion scale, suggesting that clumped disturbances are rarer in the boreal (infrequent fires) compared to clumped disturbances in the coastal zone (wind), however at the class level contagion was higher in the boreal (Fig. S3), resulting from limiting landscapes to those which explicitly contain a disturbance. In general, at the class level, mean contagion values level off rapidly and stay consistent regardless of window size, with substantial variance between ecoregions (Fig. S3). This suggests that the shape of an individual disturbance event is captured even at a relatively small extent around those disturbances (the landscape extent; see also the ratio analysis and Fig. 7, below).

Contagion (standard deviation)

Increasing variance in contagion at broader scales (Fig. 5) indicates that increasing landscape sizes are incorporating multiple disturbance extents and potentially multiple disturbance types. Ecoregions characterized by large natural disturbances (the boreal) had

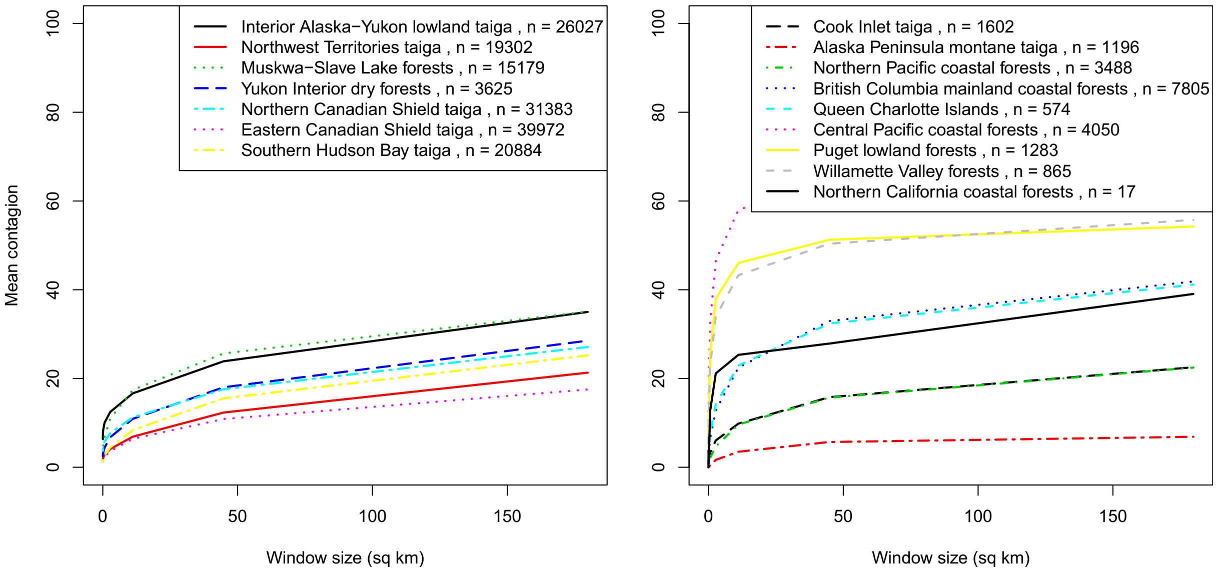

Fig. 4 Ecoregion level variation in mean contagion as a function of landscape extent. Generally, the trend is increasing even at the largest landscape sizes, indicating that less frequent, large disturbances are continuing to be included at the broadest extents. Sample size indicates number of points per ecoregion; each point measured at all scales

relatively high variance even at large extents likely because at smaller extents, primarily background mortality was detected but larger extents incorporated infrequent but large disturbances. In contrast, variance declined at the largest extents in coastal forests. The decline was quite rapid for human dominated, management-heavy systems (e.g., Central Pacific coastal forests). This suggests that the shape of disturbances is relatively better categorized by large landscapes in these regions.

Standard deviation remains relatively unchanged as landscape extent increases regardless of ecoregion at the

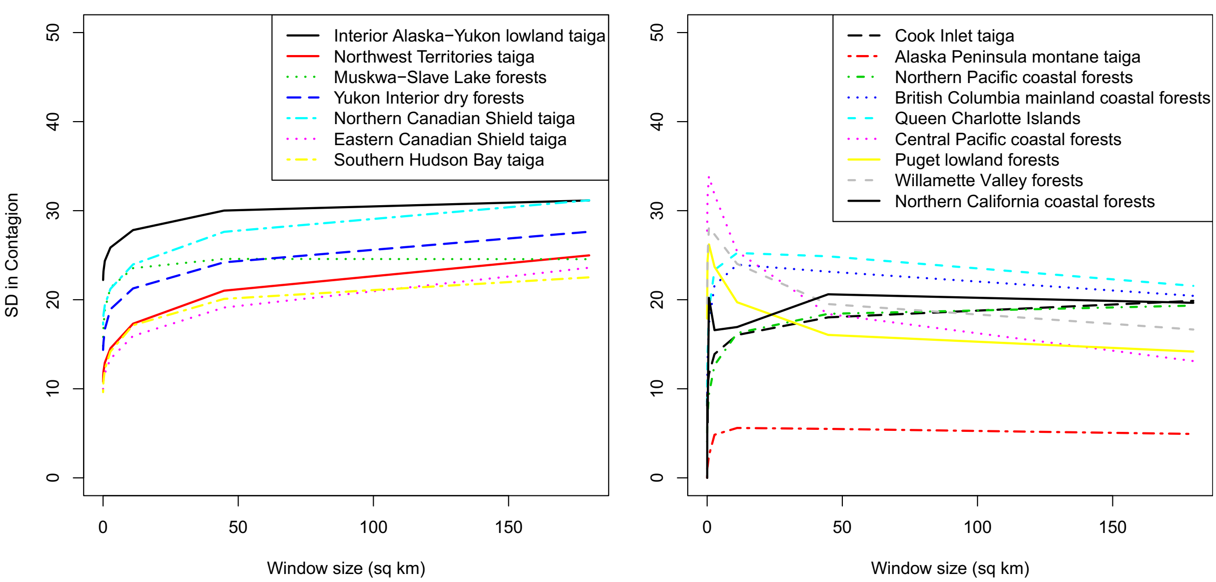

Fig. 5 Ecoregion level standard deviation of contagion values. A general increasing trend in the boreal suggests that larger extents are including relatively infrequent, broad-scale disturbances. The declining trend in coastal forests suggests that broad landscape extents do begin to encompass the range of disturbances found in their respective ecoregions and thus differences between landscapes become less prominent. Sample sizes same as Fig. 4

class level, though there is substantial spread between ecoregions (Fig. S4).

Minimizing variance within an ecoregion

The extent required to reliably reduce variance in percent disturbed between any two landscapes varied per ecoregion (Fig. 6), with some areas requiring very large extents compared to others where relatively small extents were required. This was assessed by comparing the landscape size required to reduce standard deviation within an ecoregion below a threshold acceptable value (10% chosen arbitrarily for display purposes, the Supplementary Data contains standard deviations for all landscape sizes and can be used to define any threshold for any particular ecoregion). Of the 150 ecoregions considered, 128 had extents which met this 10% threshold. Trivially, ecoregions with relatively little forest had only minimal extents required as the majority of the landscape is unforested. Of the primarily forested systems, the largest extents required were in boreal systems (> 180 km^2). The heavily managed forests of the Pacific Northwest and South, despite having similar proportion disturbed as the boreal, required significantly less landscape sizes to achieve minimal variance between landscapes (~ 10–40 km^2). The northern Pacific Northwest forests, where management is minimal and the disturbance regime is primarily small gap dynamics with no fire, had low extents required (< 1 km^2).

Ratio analysis (class scale only)

All regions follow a similar pattern of increasing contagion initially with relatively consistent disturbed area, then a leveling off of contagion and a declining mean proportion disturbed (Fig. 7). However, the initial points and the inflection point (where mean contagion stops rising and mean percent disturbed begins decreasing) are different for each ecoregion. The initial points are indicative of the mean fine-scale (90×90 m; 0.0081 km^2) disturbance contagion; isolated, single pixel disturbances would be low mean proportion (minimum of 30×30 m) and thus low contagion, whereas larger mean disturbances would have a higher proportion of that neighborhood disturbed. The inflection point (the hook in the graph) is interpreted as the scale in which the mean disturbance event is completely encompassed by the landscape extent, and so contagion remains constant while the proportion disturbed declines as the study area expands and incorporates more and more surrounding (likely undisturbed) area.

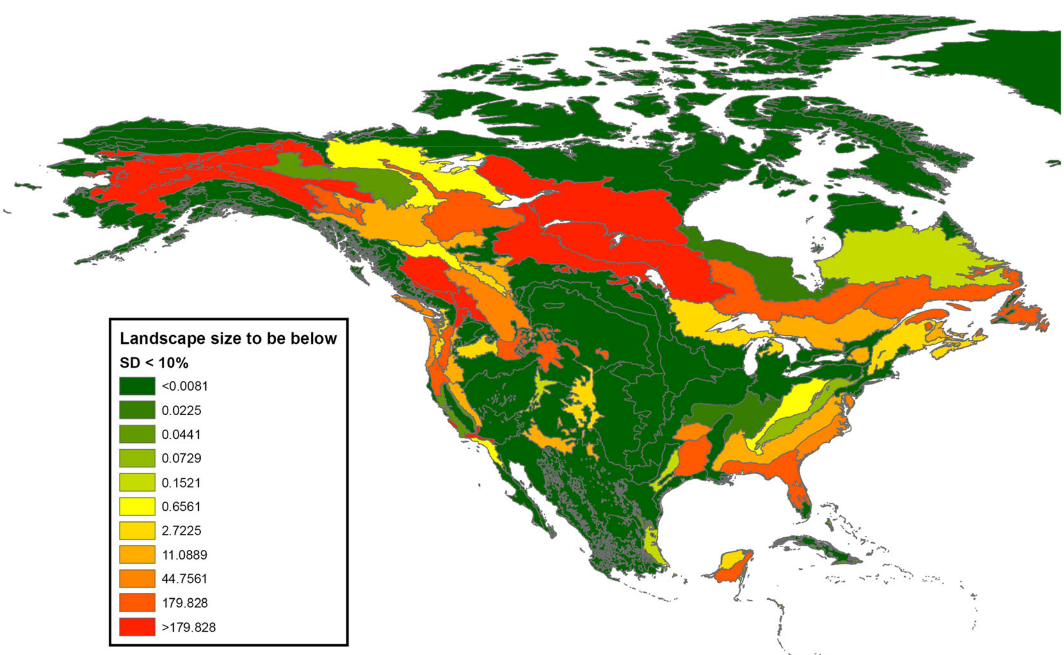

Fig. 6 Minimum landscape extent to be below 10% SD in terms of proportion disturbed. Ten percent is an arbitrary cutoff for display purposes, and precise values and contagion for each ecoregion, and at each investigated extent, are included in the supplementary data table so any cutoff can be determined

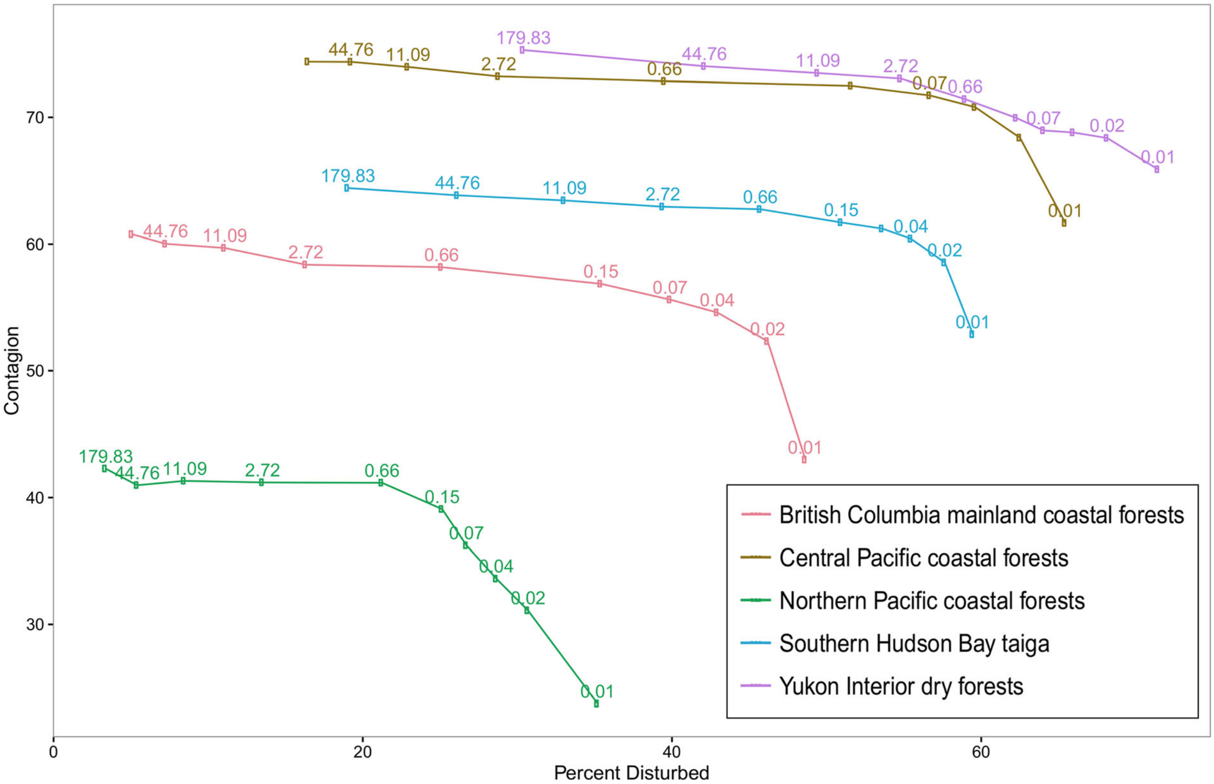

Fig. 7 Class level analysis of proportion disturbed vs. contagion. The inflection point is interpreted as the mean extent where the typical disturbance event is captured (contagion stops changing) and proportion disturbed decreases as generally undisturbed area surrounding the event is included. Example landscapes from both the boreal interior and coastal wet forest types shown. Numbers refer to the landscape extents (some numbers not shown due to overlap)

Generally, the wet forests have both a lower percent disturbed and a lower clumped value, indicating more dispersed, smaller disturbances; the boreal ecoregions have larger, more clumped disturbance regimes. A notable exception is the central Pacific coastal forest ecoregion which is similar to boreal, fire dominated regimes in terms of the relationship between disturbed proportion and disturbance shape. A landscape scale analysis is not informative for this metric, as disturbed area does not vary across the range of landscape extents (Fig. 1), and so is not shown.

The entire dataset, including mean and observed and descriptive variance (standard deviation, kurtosis, etc.) at each investigated scale and for all ecoregions in North America is available as Supplementary Data.

Discussion

Quantifying the general landscape extent at which disturbances are approximately consistent within an ecoregion is useful to the decision-making process because at this scale, the landscapes can be considered representative of the entire ecoregion with respect to disturbance processes.

This study quantifies the minimum landscape extent at which this is true for ecoregions across North America. Our results show that generally, in most ecoregions, as expected, variability between landscapes within an ecoregion in terms of proportion disturbed was reduced as landscape extent increased. In gap dominated ecoregions like the North Pacific coast and upper US Midwest, relatively small landscapes (e.g., < 10 km^2) can be selected at random and be expected to represent the overall ecoregion in terms of proportion disturbed, as indicated by the low standard deviation between the entire samples of potential landscapes. Many of these landscapes are predominantly tree-less, a trivial case, such as the Great Plains ecoregions in the central USA where percent forest cover is low and both disturbances and variability are constrained. However, some are primarily forest, such as the North Pacific coastal area, which has several predominantly forested ecoregions.

These ecoregions, primarily gap dominated areas with little fire, display a relatively consistent distribution of disturbance events, such that small landscapes chosen at random will encompass a similar amount of disturbed area. This confirms that relatively small landscapes will maintain representative amounts of disturbed/recovering areas and may function as a means to monitor changes in frequency in the future. Other ecoregions had high variability even at the broadest scale, with standard deviations between landscapes > 10% even at scales of approximately 180 km^2. These ecoregions, predominately boreal, are dominated by infrequent but large fires such that even large landscapes may be consumed in a single event. Accommodating that scale of disturbance is a serious challenge (Baker 1992). These trends were consistent regardless of whether the study location was focused on the entire ecoregion or on disturbance events (class level).

Contagion tended to increase, even at the largest extents, for ecoregions generally considered to have large disturbances, such as the boreal forest systems. This likely results from the strong impact of rare, large events (e.g., fire) contrasted against ongoing, fine-scale mortality processes, which have a very different contagion value. Because contagion is a ratio of interior to exterior edges in the overall disturbance pattern on any given landscape and is not scaled relative to landscape extent, the occasional large disturbance results in a larger contagion value. This hypothesis is supported by the gap-dynamic system comparisons, where the standard deviation decreased at broad scales, suggesting that the variety of shapes of disturbance was being successfully incorporated. These systems do have a constrained distribution of disturbance sizes, with very few large disturbance events observed (Buma and Barrett 2015). It should be noted that normalizing by average values at each scale (the coefficient of variation, see Supplementary Data Table for all ecoregions) does result in declining standard deviation across scales (Fig. S5). These results suggest that for the boreal systems, and others with large, infrequent disturbances, the examined landscape extents were not large enough to reduce actual variability in contagion.

The heavily managed ecoregions had their own pattern, with high variability in percent disturbed at small extents and rapidly declining deviations at broader scales. We hypothesize this is because small-extent landscapes will either be in unharvested or harvested areas, with very different disturbance processes and shapes, but larger landscapes appear to reflect the regular pattern of harvest which dominates these systems (the central Pacific coastal systems, Fig. 7). This change in pattern as a function of scale has been noted using fractal dimension on smaller landscapes (Mladenoff et al. 1993) and would be a useful test of management patterns designed to mimic natural dynamics to foster resilience and resistance to uncertain future disturbance drivers (O'Hara and Ramage 2013). At coarse scales, harvest designed to mimic wildfire patterns in eastern boreal ecoregions has been considered successful in emulating most natural patterns emerging from fire, though energy extraction has not (Pickell et al. 2013). The fact that heavily managed (via clearcutting) coastal forests resemble this pattern as well across all scales (Fig. 7), despite a different natural disturbance regime, suggests that current management is not mimicking natural disturbance patterns across scales (Zurlini et al. 2007). Complex socio-ecological systems not focused on forest harvest have their own disturbance-scale signatures (Zurlini et al. 2006), emerging from the interactions between humans, anthropogenic disturbance and preservation activities, and natural disturbances (which also interact with human infrastructure). Comparing these scale dependent patterns between localities within the same ecoregion may be a useful way to contrast urban and exurban development design.

The disturbance types that predominant in the example areas are generally not species specific, which may limit the variation in pattern. Ecoregions impacted by disturbances which have a specific species (or group of species) of effect, like mountain pine beetle, are likely more fine grained with the pattern reflecting the distribution of host species more than the disturbance driver (e.g., a windstorm) directly. There is also strong variability in patterns of topography which control the spatial arrangement of ecoregions and thus constrain disturbance patterning, especially when considering scaling patterns. Thus, comparisons across ecoregions must be made cautiously. In addition, some of the broad patterns (e.g., extensive disturbances in the boreal) are intuitive. However, the primary purpose of this work is to inform quantitative decision-making and research at the individual ecoregional level. The utility of these results is the ability for interested researchers, managers, conservationists, and others interested in accommodating or planning for disturbances to compare their expected scale of investigation or planning to expected disturbance proportion or variability for their respective ecoregion. It should be noted that this study describes spatial variation for the observed time period and current disturbance drivers. Climate change has complex, and often conflicting, effects on the various drivers of disturbances (Dale et al. 2000). To the extent that disturbance regimes change in the future, the current ecoregion characteristics described here may shift as well.

Combined, the two major metrics (percent disturbed and contagion) are useful at describing independent aspects of ecoregion disturbance regime characteristics across scales, one of which describes disturbance extent directly compared to landscape extent (proportion disturbed) and one that describes a fundamental disturbance characteristic (contagion) within each scale. Variation in proportion disturbed between landscapes declines quicker than contagion. Contagion did decline at the largest landscape extents in the gap dominated systems, but not in the more disturbed boreal systems (Fig. 5). These data indicate that large landscapes are better able to represent the proportion disturbed of a given ecoregion more easily than contagion. The implications of this depend on the application and system—if the goal is to represent land cover types, and their arrangement is less significant, than proportion disturbed is a good metric. If the goal is representation of emergent aspects of shape, such as edge or interior habitat associated with disturbance, then larger extents appear to be needed.

Limitations and considerations

Disturbance return intervals are often significantly longer than the time period of historical record, and continental-scale, high resolution mapping of disturbance as utilized here date from 2000, and the satellite record from the 1970s. Thus, this study takes advantage of the complete view of each ecoregion to establish an approach similar to a space-for-time chronosequences, where we assume that disturbance frequencies (since 2000) across an entire ecoregion are consistent with the historical normal rates. However, multi-decadal climate fluctuations which extend beyond our time period of observation can drive disturbance frequencies in some locations, such as synchronicities between the El Nino Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the Atlantic Multidecadal Oscillation (AMO; Schoennagel et al. 2007). If the entire spatial extent of the ecoregion is influenced by these cycles simultaneously, then a longer time period of observation would be useful. However, these results are still valuable in that they represent a range of broad climate drivers, for example, covering a period of changing PDO and ENSO values. In addition, they also provide a baseline by which to accommodate future shifts—for example, in areas where disturbance size is likely to decrease (e.g., more frequent, smaller fires), a smaller extent may be necessary. Finally, when longer time series are available, comparison to this dataset will be a useful tool for identifying long-time period, broad-scale disturbance cycles which would be observable as deviations from the normal in terms of extent or shape.

Secondly, the combination of very broad extents and very fine resolutions inherently results in some level of speculation about actual drivers of observed patterns at any single, specific location on the landscape. There has been success using broader-scale (less specific) ecoregions for research on the mechanisms behind single disturbance processes (e.g., fire, Hawbaker et al. 2013). Because we desired to include comprehensive disturbance regimes, it is not feasible to mechanistically model individual drivers of disturbances (and some drivers for one disturbance type may inhibit others). It is likely that various mechanisms are producing the ecoregion level patterns observed here, and multiple disturbance types in some regions likely enhance the variance; one could hypothesize that ecoregions with one typical disturbance driver (e.g., wind) would have little variance in pattern metrics, whereas ecoregions with a variety of disturbance types and processes (e.g., wind, pests, and fire) would have higher variance. The purpose of this publication is to quantify on patterns in each ecoregion, provide data, and suggest ways in which the data may be useful to researchers, managers, and policy makers working in those regions, who can then make determinations about specific mechanisms.

Conclusions

Quantifying the minimum size of a "representative landscape" within any given ecoregion is important for research and management of any disturbance-sensitive process, such as conservation planning, development, or carbon accounting. This is especially true for objectives which require incorporation of future disturbances, which will occur in unknown locations yet must be considered, such as conservation/reserve designs which seek to include natural disturbance regimes. These regimes are characteristic parts of an ecosystem and implicit in ecoregional classifications which often guide management decisions, but have never been quantified in a scale-explicit manner. Knowing the requisite extent for a landscape to incorporate those anticipated, but unknown, events is crucial. Here we presented the first simultaneous quantification of these scale-variance relationships for disturbance proportion and cohesion, two important spatial aspects of a disturbance regime. That size varies depending on ecoregion, from relatively small extents in gap dominated forests to very large extents, in the fire-influenced boreal forests and incorporates variation driven by topographical constraints on forest distribution or disturbance behavior. Management-dominated systems have a specific signature associated with significant proportions disturbed but relatively low variance spatially. The key purpose of this research is to provide users with the resources to make scale-informed decisions about disturbance processes on their ecoregion of study.

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