Understanding the importance of small patches of habitat for conservation

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Summary

1. Conservation activities in fragmented landscapes have largely focused on keeping remaining large patches intact, often disregarding the increasingly important role of smaller patches in the conservation of remaining vegetation. As habitat loss proceeds in fragmented landscapes, there is an increasing need to measure the relative contribution of all patches (large and small) to overall ecosystem persistence, in a way that helps deliver effective conservation strategies aimed at preventing the death of ecosystems by a thousand cuts.

2. Using Australian vegetation communities as a case study, we calculated the historical change in the contribution of patches below different sized thresholds to overall extent. We introduced a new patch assessment metric based on the Gini coefficient that indicates how unequal the distribution of patch sizes is relative to historical distributions.

3. At least 22% of major vegetation communities in Australia have >50% of their remaining extent in patches <1000 ha. Loss does not always match fragmentation status: though some vegetation communities are exposed to the double jeopardy of high loss and high fragmentation, others are far more affected by fragmentation than loss of extent.

4. For some communities, actions focused on protecting large patches are critical but for many others, protecting and managing small patches is crucial for community persistence.

5. Synthesis and applications. Arbitrary patch size thresholds for permitting native vegetation clearing are dangerous for ecosystems whose distribution is now restricted to small patches. We recommend that clearing thresholds be scaled to reflect the fact that some ecosystems are more dominated by small patches than others. With a renewed focus on formally assessing the threat status of ecosystems as well as species, ecosystem accounts such as those demonstrated in this study are the first step to reliably assessing vulnerability. Measures of ecosystem vulnerability that only consider the extent of vegetation loss and not the size of remaining patches are likely to be ineffective for impact assessment, conservation planning and preventing ecosystem loss.

Key-words: Australia, environmental accounts, fragmentation, Gini Index, habitat area, IUCN Red List of Ecosystems, land-clearing policy, National Vegetation Information System, patch size, threatening processes

Introduction

Despite significant attempts to protect ecosystems from large-scale clearance via conservation actions such as protected areas (Watson et al. 2014) and compensation schemes (Grieg-Gran 2006; Combes Motel, Pirard & Combes 2009), more than 80% of the terrestrial world has been modified by human activities (Sanderson et al. 2002). At the global scale, almost all ecosystems are declining in total extent, as well as becoming increasingly fragmented (Saunders, Hobbs & Margules 1991; Fischer...
Importance of small patches for conservation

& Lindenmayer 2007; Laurance et al. 2011). Consequently, small patches are now not only a common feature in many landscapes, but also represent an increasingly large component of remaining habitat in many ecosystems.

The last two decades have seen a large body of ecological theory and field research highlighting the role of large patches of vegetation in enabling habitat-dependent species persistence (Andren 1994; Bender, Contreras & Fahrig 1998; Fischer et al. 2009). The importance of maintaining large patches is repeatedly emphasized in theory (MacArthur & Wilson 1967) and practice (Ferraz et al. 2007; Mortelliti et al. 2014). Species-area relationships (Rosenzweig 1995), patch size-population density relationships (Connor, Courtney & Yoder 2000) and assessments of the impact of edge effects on patch size (Beier, Van Drielen & Kankam 2002; Watson, Whittaker & Dawson 2004) all support large contiguous habitat blocks. A consequence of this wealth of evidence has been that conservation-oriented actions in fragmented landscapes (e.g. vegetation legislation, offset design and best-practice agricultural land management) have been almost ubiquitously framed around keeping remaining large patches intact, and ensuring connectivity between large patches is created or maintained. These actions are no doubt important for maintaining biodiversity, but a singular focus on keeping large patches intact and well-connected can mean that smaller patches are overlooked in landscape conservation (but see Ovaskainen 2002). Simply by maintaining geographic extent, small patches contribute to short- and long-term species persistence, but are often the most vulnerable to land clearing. For instance, landholders in many countries (e.g. Brazil, Canada, Australia and New Zealand) are allowed to routinely clear small (<1 ha) vegetation patches without permits or vegetation assessments being conducted (Stobbe, Cottелеer & Cornelis Van Kooten 2009; Stickler et al. 2013; Taylor 2013).

As the erosion and fragmentation of vegetated landscapes continues (Hansen et al. 2013), a better understanding of the relative roles of smaller patches in conservation strategies is needed. Vulnerability of a given ecosystem is traditionally assessed via loss of extent (Nicholson, Keith & Wilcove 2009; Keith et al. 2013), usually by measuring the total proportion of that community that has been removed (e.g. global forest assessments; FAO 2012; Keith et al. 2013). There are currently no widely accepted or effective solutions to account for the influence of the spatial arrangement of available habitat (such as the relative contribution of small or large patches) on ecosystem persistence and vulnerability (Smith et al. 2009; Wang & Cumming 2011). Assessing the importance of variable patch sizes to ecosystem persistence could provide planners with guidance on the size and number of small patches that should be managed. This might assist with protecting minimum habitat targets for species of conservation concern (Goldingay & Possingham 1995), or assessing the amount of clearing of small patches that an ecological community might tolerate before risk of ecosystem collapse due to accumulated loss of extent. Reliable metrics accounting for both loss of extent and patch contribution are needed to understand the pace of habitat loss and landscape beta-diversity change, assess ecosystem vulnerability and make decisions about where and if protection or vegetation clearing should be permitted (Villard & Metzger 2014). Without considering these metrics, we risk continuous erosion of small patches and the slow, inevitable decline of vegetation communities and the species dependent on them for their persistence: a death by a thousand cuts.

Here, we provide two new measures of vegetation change that consider the relative size of remaining vegetation patches. Using data on vegetation clearing in Australia, we evaluate the amount of fragmentation that has occurred to vegetation communities by accounting for (i) the importance of small patches and (ii) patch inequality, which are comparable between communities and take into account historical baselines. We compare these two patch-related measures with a traditional measurement of vegetation community loss of extent. In doing so, we assess the vulnerability of vegetation communities to both total loss and fragmentation and as such provide a case study of the contribution of small patches to conservation outcomes.

Materials and methods

CASE STUDY

Our case study is the megadiverse continent of Australia (Mittermeier, Mittermeier & Gil 1997), chosen because (i) data are available on the distribution and size of vegetation patches both today and historically; and (ii) widespread recent (within the past 200 years) vegetation clearing has led to serious biodiversity issues across many parts of the continent (Lindenmayer 2007; Kingsford et al. 2009). We defined vegetation communities according to the Australian Government’s National Vegetation Information System (NVIS 4.1, Australian Government Department of Sustainability, Environment, Water, Population and Communities). This unique raster data set summarizes Australia’s present (extant) native vegetation, classified into 85 Major Vegetation Subgroups (nv1s MVS 4.1) at 100 × 100 m (1 ha) resolution, with a comparable estimated pre-1750 (pre-European, pre-clearing) data set also available. We excluded all non-vegetation and cleared vegetation types (e.g. freshwater, seas), resulting in a final list of 75 vegetation communities.

RATE OF CLEARING OF NATIVE VEGETATION

We estimated the relative change in total original extent that each vegetation community has undergone since European settlement of Australia (from now on termed ‘pre-1750’). We then derived the total area (in square kilometres) covered by each classified NVIS MVS from the maps of pre-1750 and extant vegetation and calculated the percentage change between these two values for each community.
ACCOUNTING FOR SMALL PATCH CONTRIBUTIONS TO REMAINING EXTENT

To determine the number and size of patches in each vegetation community, we converted the raster layers of pre-1750 and extant NVIS MVs to individual polygons and calculated the area of each polygon. For each pre-1750 and extant vegetation community, we ranked patches in ascending order of size, calculated the cumulative area for each community based on patch rank and derived the proportional cumulative area of every patch (for supporting code see Appendix S2 in Supporting Information). Patches were defined as a contiguous polygon not directly connected to any other polygon of the same vegetation type.

We explored the ability of two simple approaches to account for small patch contribution to remnant vegetation, in relation to a historical baseline. First, we set patch size thresholds across all vegetation communities, below which the patch is considered small and therefore vulnerable to clearing. Fixed thresholds are easy to explain, quickly reduce uncertainty and are therefore commonly used in decision-making (Huggett 2005; Nicholson, Keith & Wilcove 2009), such as for permissible deforestation on private land (McAlpine, Fensham & Temple-Smith 2002). Our first metric describes the relative change between the pre-1750 and current contribution (C) of small patches to the total extent of a given vegetation community. To calculate this, we used the following formula:

\[ C(a) = P_1(a) - P_0(a), \]

where \( P_1 \) is a value between zero and one representing the proportion of the extant vegetation community extent made up of patches that are smaller than the threshold patch area \( a \), and \( P_0 \) is a value between zero and one representing the proportion of the original (baseline) vegetation community extent made up of patches that are smaller than \( a \). A value of zero represents no change, whereas a value of 1 indicates that all patches are now smaller than the threshold. We calculated the proportion of the original and remaining extent of each vegetation community that consisted of patches smaller than thresholds of 1, 2, 5, 10, 20, 50, 100, 1000, 5000, 10 000 and 100 000 ha. We report results for a threshold of 5000 ha in the main text. We do not know the minimum critical area of habitat required by most species in Australia, but between 1000 and 5000 ha of effective habitat is considered to be a reasonable area for maintaining species genetic diversity in Australia (Lancaster et al. 2011) as well as preventing mammal population extinctions both in Australia (Goldingay & Possingham 1995; Jackson 1999; Nicholson et al. 2006) and in other parts of the world (Ferraz et al. 2007; Mortelliti et al. 2014).

Because thresholds are arbitrary (Maron et al. 2012), we compared our patch contribution measure based on thresholds with a measure based on patch inequality that accounts for all patch sizes and their relative contribution to the overall extent of a vegetation community. The Gini coefficient is the most widely known and used measure of inequality in economics (Allison 1978), and it measures the difference between a perfectly equitable distribution and the actual distribution of a resource. Recently, the Gini coefficient was proposed as a way for establishing the level of equality of protection across the world’s terrestrial ecoregions within 83 countries (Barr et al. 2011). Because it is bound between zero (most even) and one (least even), it is easy to interpret and communicate to planners and policymakers.

We investigated whether the Gini coefficient could be adapted to evaluate landscape spatial configuration of remnants, by measuring equity in the distribution of patch sizes within any given vegetation community.

We calculated a Gini coefficient for each extant and 1750 vegetation community using Brown’s (1994) formula:

\[ G = 1 - \sum_{i=0}^{n-1} (Y_{i+1} + Y_i)(X_{i+1} - X_i), \]

where \( X_i \) is the cumulative proportion of \( n \) remnants in the vegetation community, for \( i = 1, \ldots, n \), and \( Y_i \) is the cumulative proportion of the current area of \( n \) remnants in the vegetation community, for \( i = 1, \ldots, n \). We then derived the change in the Gini coefficient (\( \Delta G \)) between current and baseline conditions:

\[ \Delta G = G_1 - G_0, \]

where \( G_1 \) is the Gini coefficient for the current (extant) vegetation community, and \( G_0 \) is the Gini coefficient for the historical (pre-1750) vegetation community. This metric takes a value between \(-1\) and 1. A negative value represents communities becoming more equal in patch size distribution; a positive value represents less equality in patch size distribution.

All statistical analyses were performed in R version 3.1.1 (R Core Team 2014), and all spatial analyses were conducted in ESRI ARC GIS version 10.0.

Results

LOSS OF VEGETATION COMMUNITY EXTENT

Many communities have been heavily cleared (Tables 1 and 2), but vegetation clearing has not impacted all communities equally (Fig. 1a), nor is it occurring at equal rates across the continent (Fig. 2a). In Australia, 24 broad vegetation communities (32% of the 75 evaluated) have lost at least 20% of their original extent, and seven communities (9%) have lost >40% of their original extent. Many of those most heavily cleared occur in the agriculturally productive coastal regions of Australia (Fig. 2a). The three most heavily cleared communities (mallee with a tussock grass understory, Brigalow and temperate tussock grasslands), together previously covered more than 170 000 km² of Australia, and each has <20% of their original extent remaining (Table 1). In comparison, 19 (25%) vegetation communities have lost a very small (<2%) proportion of their original extent (Fig. 1a).

Vegetation communities were not distributed equally in their original areal extent (Table 1). Original vegetation cover ranged over 4-6 orders of magnitude across vegetation communities (Fig. 3a). There is no consistent relationship between original extent and proportional loss (linear regression: \( R^2 = 0.02; F = 1.38, d.f. = 1,733, P = 0.24 \)). For example, Banksia woodlands originally covering approximately 7300 km² of Australia have lost almost 50% of their extent. In contrast, cool temperate rainforest originally covered a similar area (8175 km²) and has lost <5% of its extent.
Table 1. Results of metrics per Australian vegetation community (NVIS major vegetation groups), showing top 20 for loss of extent, change in proportion of patches smaller than 5000 ha and Gini metric (for NVIS codes and additional patch size thresholds see Supporting information)

<table>
<thead>
<tr>
<th>Vegetation community</th>
<th>pre-1750 area (km²)</th>
<th>% Loss of extent</th>
<th>Rank loss of extent</th>
<th>Number of pre-1750 patches</th>
<th>% Change in number of patches &lt; 5000 ha C (5000)</th>
<th>Proportion change in number of patches</th>
<th>Rank threshold</th>
<th>Gini metric ΔG</th>
<th>Rank Gini</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mallee with a tussock grass understorey</td>
<td>60 484</td>
<td>97.3</td>
<td>1</td>
<td>16 309</td>
<td>1.3</td>
<td>0.86</td>
<td>1</td>
<td>-0.161</td>
<td>1</td>
</tr>
<tr>
<td>Brigalow forests and woodlands</td>
<td>96 493</td>
<td>86.9</td>
<td>2</td>
<td>48 618</td>
<td>379.7</td>
<td>0.66</td>
<td>3</td>
<td>-0.061</td>
<td>4</td>
</tr>
<tr>
<td>Temperate tussock grasslands</td>
<td>16 594</td>
<td>81.7</td>
<td>3</td>
<td>38 494</td>
<td>150.2</td>
<td>0.68</td>
<td>2</td>
<td>-0.159</td>
<td>2</td>
</tr>
<tr>
<td>Open mallee woodlands and sparse mallee shrublands with a tussock grass understorey</td>
<td>1904</td>
<td>70.7</td>
<td>4</td>
<td>7 531</td>
<td>0.7</td>
<td>0.08</td>
<td>19</td>
<td>-0.098</td>
<td>3</td>
</tr>
<tr>
<td>Banksia woodlands</td>
<td>7327</td>
<td>49.5</td>
<td>5</td>
<td>8 361</td>
<td>302.7</td>
<td>0.20</td>
<td>5</td>
<td>-0.028</td>
<td>10</td>
</tr>
<tr>
<td>Eucalyptus woodlands with a tussock grass understorey</td>
<td>725 124</td>
<td>46.8</td>
<td>6</td>
<td>583 880</td>
<td>88.6</td>
<td>0.14</td>
<td>8</td>
<td>-0.018</td>
<td>18</td>
</tr>
<tr>
<td>Casuarina and Allocasuarina forests and woodlands</td>
<td>28 232</td>
<td>44.3</td>
<td>7</td>
<td>70 911</td>
<td>12.7</td>
<td>0.09</td>
<td>14</td>
<td>-0.025</td>
<td>14</td>
</tr>
<tr>
<td>Low closed forest or tall closed shrublands (including Acacia, Melaleuca and Banksia)</td>
<td>28 900</td>
<td>39.2</td>
<td>8</td>
<td>73 603</td>
<td>5.7</td>
<td>0.06</td>
<td>24</td>
<td>-0.027</td>
<td>11</td>
</tr>
<tr>
<td>Tropical or subtropical rainforest</td>
<td>21 037</td>
<td>37.8</td>
<td>9</td>
<td>61 373</td>
<td>13.5</td>
<td>0.17</td>
<td>6</td>
<td>-0.037</td>
<td>7</td>
</tr>
<tr>
<td>Open mallee woodlands and sparse mallee shrublands with a dense shrubby understorey</td>
<td>7827</td>
<td>37.3</td>
<td>10</td>
<td>7997</td>
<td>12.6</td>
<td>0.13</td>
<td>10</td>
<td>-0.021</td>
<td>16</td>
</tr>
<tr>
<td>Blue grass and tall bunch grass tussock grasslands</td>
<td>28 988</td>
<td>36.8</td>
<td>11</td>
<td>14 753</td>
<td>45.9</td>
<td>0.15</td>
<td>7</td>
<td>0</td>
<td>45</td>
</tr>
<tr>
<td>Eucalyptus woodlands with ferns, herbs, sedges, rushes or wet tussock grassland</td>
<td>16 430</td>
<td>35.5</td>
<td>12</td>
<td>84 922</td>
<td>52.1</td>
<td>0.08</td>
<td>17</td>
<td>-0.048</td>
<td>5</td>
</tr>
<tr>
<td>Dry rainforest or vine thickets</td>
<td>15 720</td>
<td>35.4</td>
<td>13</td>
<td>33 191</td>
<td>10.5</td>
<td>0.02</td>
<td>34</td>
<td>-0.03</td>
<td>9</td>
</tr>
<tr>
<td>Other shrublands</td>
<td>99 063</td>
<td>32.2</td>
<td>14</td>
<td>78 168</td>
<td>80.2</td>
<td>0.11</td>
<td>13</td>
<td>-0.011</td>
<td>22</td>
</tr>
<tr>
<td>Eucalyptus woodlands with a shrubby understorey</td>
<td>390 075</td>
<td>30.3</td>
<td>15</td>
<td>298 578</td>
<td>71.1</td>
<td>0.08</td>
<td>16</td>
<td>-0.011</td>
<td>23</td>
</tr>
<tr>
<td>Mallee with an open shrubby understorey</td>
<td>57 075</td>
<td>27.3</td>
<td>16</td>
<td>68 323</td>
<td>48.9</td>
<td>0.05</td>
<td>27</td>
<td>-0.007</td>
<td>30</td>
</tr>
<tr>
<td>Eucalyptus open woodlands with a grassy understorey</td>
<td>193 898</td>
<td>26.5</td>
<td>17</td>
<td>168 772</td>
<td>42.4</td>
<td>0.05</td>
<td>28</td>
<td>-0.005</td>
<td>33</td>
</tr>
<tr>
<td>Open mallee woodlands and sparse mallee shrublands with an open shrubby understorey</td>
<td>4230</td>
<td>25.1</td>
<td>18</td>
<td>3362</td>
<td>95.8</td>
<td>0.06</td>
<td>21</td>
<td>0.012</td>
<td>72</td>
</tr>
<tr>
<td>Saline or brackish sedgelands or grasslands</td>
<td>1259</td>
<td>24.9</td>
<td>19</td>
<td>7970</td>
<td>2.1</td>
<td>0.12</td>
<td>12</td>
<td>-0.031</td>
<td>8</td>
</tr>
<tr>
<td>Other Acacia forests and woodlands</td>
<td>111 049</td>
<td>23.3</td>
<td>20</td>
<td>70 660</td>
<td>14.0</td>
<td>0.06</td>
<td>23</td>
<td>-0.009</td>
<td>27</td>
</tr>
<tr>
<td>Eucalyptus (+/- tall) open forest with a dense broad-leaved and/or tree fern understorey (wet sclerophyll)</td>
<td>28 539</td>
<td>19.9</td>
<td>24</td>
<td>228 279</td>
<td>5.6</td>
<td>0.22</td>
<td>4</td>
<td>-0.039</td>
<td>6</td>
</tr>
</tbody>
</table>
Table 1. (Continued)

<table>
<thead>
<tr>
<th>Vegetation community</th>
<th>pre-1750 area (km²)</th>
<th>% Loss of extent</th>
<th>Rank loss of extent</th>
<th>Number of pre-1750 patches</th>
<th>% Change in number of patches &lt;5000 ha C (5000)</th>
<th>Rank threshold</th>
<th>Gini metric ΔG</th>
<th>Rank Gini</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eucalyptus tall open forests and open forests with ferns, herbs, sedges, rushes or wet tussock grasses</td>
<td>43 209</td>
<td>19.3</td>
<td>25</td>
<td>188 514</td>
<td>20.1</td>
<td>0.14</td>
<td>9</td>
<td>−0.026</td>
</tr>
<tr>
<td>Eucalyptus open forests with a shrubby understorey</td>
<td>117 521</td>
<td>21.6</td>
<td>23</td>
<td>417 050</td>
<td>19.1</td>
<td>0.12</td>
<td>11</td>
<td>−0.026</td>
</tr>
<tr>
<td>Tropical mixed species forests and woodlands</td>
<td>10 161</td>
<td>−12.2</td>
<td>74</td>
<td>11 197</td>
<td>126.1</td>
<td>0.08</td>
<td>15</td>
<td>−0.013</td>
</tr>
<tr>
<td>Eucalyptus open forests with a grassy understorey</td>
<td>177 016</td>
<td>17.8</td>
<td>27</td>
<td>456 194</td>
<td>10.1</td>
<td>0.08</td>
<td>18</td>
<td>−0.016</td>
</tr>
<tr>
<td>Mallee with a dense shrubby understorey</td>
<td>91 555</td>
<td>22.6</td>
<td>21</td>
<td>99 032</td>
<td>53.3</td>
<td>0.07</td>
<td>20</td>
<td>−0.011</td>
</tr>
<tr>
<td>Eucalyptus tall open forest with a fine-leaved shrubby understorey</td>
<td>9220</td>
<td>12.6</td>
<td>31</td>
<td>138 724</td>
<td>−2.2</td>
<td>0.05</td>
<td>29</td>
<td>−0.022</td>
</tr>
<tr>
<td>Casuarina and Allocasuarina open woodlands with a tussock grass understorey</td>
<td>4923</td>
<td>1.1</td>
<td>58</td>
<td>1360</td>
<td>−29.6</td>
<td>0</td>
<td>73</td>
<td>−0.021</td>
</tr>
</tbody>
</table>

Table 2. Results of paired t-tests comparing current and historical (pre-1750) mean extent and mean number of patches of 75 broad vegetation communities in Australia. For specific results of statistical differences in patch size distributions for each vegetation community, Table S5 provides results of Mann–Whitney–Wilcoxon tests.

<table>
<thead>
<tr>
<th>Community characteristic</th>
<th>Current mean (±SE)</th>
<th>Historical mean (±SE)</th>
<th>t Statistic</th>
<th>P</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extent (km²)</td>
<td>88 462 ± 20 275</td>
<td>102 132 ± 21 881</td>
<td>−2.783</td>
<td>0.003</td>
<td>74</td>
</tr>
<tr>
<td>Number of patches</td>
<td>62 057 ± 12 040</td>
<td>49 720 ± 9044</td>
<td>2.955</td>
<td>0.002</td>
<td>74</td>
</tr>
</tbody>
</table>

Fig. 1. Frequency histogram of the number of vegetation communities exhibiting a given (a) percentage change in extent and (b) change in number of patches. Communities at the far left have (a) lost the majority of their original extent or (b) lost patches. Communities at the far right (above 0) have (a) gained in extent, replacing other communities due to land management practices, or (b) increased their patchiness.

There are more individual patches per community today on average than historically (t-test *P* < 0.01, Table 2). A linear regression revealed that 22% of the variation in the increase in number of patches could be explained by loss of extent (*F = 21.07*, d.f. = 1.73; *P* < 0.01). The number of patches per community has increased since clearing began for 81% (61) of the communities despite a mean loss of 18.8% (±2.9 SE) of the extent of these 61 communities (Fig. 1b, see also Appendix S1). For instance, Brigalow formerly extended across 96 492 km² distributed amongst 10 136 patches. Today, this has been reduced by 87% to 12 665 km² distributed amongst 48 618 patches: a fourfold increase in the original number of patches despite the enormous overall decline in extent (Table 1). Conversely, for the 14 communities in which the number of patches has declined (Fig. 1b), the overall change in extent was small (mean ± S.E.: 2.8 ± 1.9%).

The importance of small patches in representing communities varied historically and today (Fig. 3b). Vegetation communities generally had less small patches and more large patches contributing to their extent pre-1750 (Table 2, Fig. 4a,b). Exceptions include cool temperate rainforest and boulders communities that were naturally patchy due to their position on the tops of mountains (Fig. 4a,b). The contribution of patches <5000 ha has increased in all parts of Australia (Fig. 2b; red, orange and yellow areas), with patches <5000 ha now comprising an equal or greater proportion of almost all the vegetation communities (Fig. 3b; Table S1). This change in the
contribution of small patches is positively related to loss of extent (linear regression: $R^2 = 0.68$; $F = 163.22$, d.f. = 1.73; $P < 0.01$).

Today, almost all of the remaining extent (95%) of ten communities is represented in patches $<10,000$ ha (Fig. 4d). This includes communities such as Brigalow (Fig. 4a), for which $<35\%$ of its extent are in patches below this 10,000 ha threshold (Fig. 4b). More than a third of the remaining extent of 35% (27) of communities is made up of patches smaller than 1000 ha (10 km²). For 13 of these (18% of all communities), the proportion comprised of patches $<1000$ ha rises to at least 50% (Fig. 4d) – originally, only eight communities (10%) had half of their extent represented by patches smaller than 1000 ha (Fig. 4c, Table S3). Four communities have at least a quarter of their remaining distribution in patches smaller than 10 ha (open mallee woodlands, Leptospermum forests and woodlands, Eucalyptus tall open forest with fine-leaved shrubby understorey, and Boulders or alpine fjaeldmarks) – despite three of these (Eucalyptus forest, Leptospermum forests and Boulders) being naturally patchy, this proportion has increased for all communities.

Comparing Gini coefficients for each vegetation community between 1750 and today (Fig. 3c) showed that 43% (33) have become more equitably distributed in terms of patch sizes (a declining Gini coefficient), 12% (9) have become less equitably distributed (an increasing Gini coefficient).
coefficient), and 45% (35) have shown <0.5% change in equitability (Table 1 and Tables S1 and S5). Communities more equitably distributed with regard to patch sizes (i.e. with a decline in the Gini coefficient) are generally a result of most of the large patches being broken up into many small patches, as these communities had a greater contribution of small patches today than historically (linear regression: $R^2 = 0.72$; $P < 0.01$; Table 1). Communities with less equitably distributed patch sizes are generally a result of small patches becoming smaller, whilst the community still maintains some big patches (Table S6).

Neither the Gini Index nor the patch contribution measure is sensitive to all forms of landscape change. In some rare cases, fragmentation occurred (with resulting increase in the contribution of small patches) but a comparison of Gini Indices between 1750 and today shows no change, when all patch sizes were fragmented equally (e.g. mulga open woodlands; Table S6). In other cases, the Gini Index shows sensitivity to change in patch distributions whilst the patch contribution measure remains constant over time, due to processes such as edge removal from all patches (e.g. dry rainforest or vine thickets; Table S6).

**RELATIONSHIP BETWEEN LOSS AND PATCH CONTRIBUTION**

Loss of extent and fragmentation have clearly not occurred evenly across all vegetation communities (Table 1 and Table S6). By ranking vegetation communities by overall loss of extent and by the change in the contribution of small patches, we were able to discover which communities did not conform to general relationships of increasing fragmentation with increasing loss of extent (Figs 2d and 3d). Some communities were impacted very...
little by either fragmentation or loss (e.g. hummock grasslands, saltbush and bluebush shrublands) and mostly occur in the arid central regions of Australia (Fig. 2d). A number of vegetation communities were subject to double jeopardy because they are being highly impacted by both loss of extent and fragmentation (e.g. mallee with a tussock grass understorey, Brigalow forests and woodlands, and Banksia woodlands; Fig. 2d), with associated increase in patch equity generally due to an increase in the overall number of small patches and loss due to fragmentation of large patches (Table 1, Fig. 4a,b). Relative to other vegetation communities, at least 17 vegetation communities were more impacted by fragmentation but less by loss (e.g. Eucalyptus open forest with a dense broad-leaved and/or tree fern understorey, mangroves), and 18 communities were more impacted by loss than fragmentation (e.g. dry rainforest or vine thickets, mallee with an open shrubby understorey; Fig. 3d; see Appendix S3).

Discussion

Fragmentation is now widespread across ecosystem types and regions. Increased clearing of vegetation communities in Australia (Fig. 3a) has led to many more individual patches in the landscape and small patches taking on increased importance (Table 2, Figs 3b and 4d). Despite increasing research focus on evaluating risks to ecosystems (Nicholson, Keith & Wilcove 2009; Keith et al. 2013), the different forms of habitat loss and fragmentation have not yet been assessed in a way that helps deliver applied conservation outcomes. We demonstrate new ways to assess the overall contribution of conserving patches of different sizes to the persistence of a vegetation community, as small patches may be crucial to species survival and community resilience (Matthews, Cottee-Jones & Whittaker 2015). In doing so, we show the importance of better evaluating the vulnerability of all vegetation communities to threatening processes, regardless of their size and extent of loss.

Many vegetation communities in Australia now occur disproportionately in small patches (Fig. 4d); at least 13 (17%) major vegetation communities in Australia mainly comprise (>30% of their current extent) patches under 1000 ha (10 km²; Fig. 4d). This figure doubles if we consider patches smaller than 5000 ha (50 km²). However, in Australia (as in many parts of the world), small-scale vegetation clearing continues at pace with few checks (Taylor 2013), leading to the gradual erosion of remaining small patches. In Australia, the only legislative trigger to prevent clearing of small patches is the presence of a species or community formally listed under the Environmental Protection and Biodiversity Conservation (EPBC) Act 1999. By the time a community is EPBC listed, many of the last remaining small patches of that vegetation may have been cleared. For example, 10 vegetation communities currently have at least 30% of their remaining extent in patches smaller than 100 ha (1 km²), an area that under some recent land-clearing legislation changes is permissible for clearing, sometimes without a permit if the community occurs on prime agricultural land (Taylor 2013). Because six of these communities have not yet suffered more than 30% loss of extent and therefore cannot be legislatively protected, legalized land-clearing can occur in such a way that it will cause significant cumulative impact to warrant listing as vulnerable under IUCN Red List guidelines (Keith et al. 2013). To adequately identify ecosystems at risk of collapse, there is a need to move away from relying solely on the amount or rates of loss and assess the overall contribution of all vegetation patches to the ecosystem’s long-term viability. By quantifying the reliance of vegetation communities on a variety of patch sizes, we show that it is possible to explicitly consider the influence of fragmentation, and the impact of clearing patches of a given size, for a given community.

As a result, environmental impact assessments and subsequent development and offset decisions could more easily take into account fragmentation implications for affected communities, and trade-offs within and between different sized vegetation communities can be considered.

The approach demonstrated here could be used to set more realistic thresholds of permissible vegetation clearing, which reflect the relative vulnerability of each community to the threat of ongoing clearance of small patches. Setting an arbitrary patch size clearance allowance where no penalties occur for clearance of small patches, as currently seems to be the case with some policy instruments (Maron et al. 2012), seals the eventual fate of all patches below that threshold. This could be especially dangerous in landscapes with low habitat nestedness, in which multiple complementary small and large patches are required to maintain species persistence (Matthews, Cottee-Jones & Whittaker 2015). Similar to setting conservation planning targets for biodiversity protection (Smith, Goodman & Matthews 2006), it might be better to equalize the proportion of remaining vegetation patches that we are prepared to lose rather than settle on a fixed area. For example, if conservationists wanted to ensure <25% of remaining vegetation is cleared whilst still allowing small patches (e.g. on prime agricultural land) to be cleared, the definition of a ‘small’ patch contributing to the permissible 25% would be highly variable (Fig. 4d). Sensitivity analyses showed that the patch size threshold below which 25% of the total extent of Australian vegetation communities occurred varied from 0.03 to 116 970 km² (Appendix S1). Permissible patch size clearing thresholds related to the percentile contribution of small patches to overall extent would allow clearance regimes to be tailored to each ecosystem, with an aim to prevent death by a thousand cuts. We believe these tailored thresholds could equally apply to current IUCN Red List of Ecosystems assessments (Rodriguez et al. 2011; Keith et al. 2013), especially around those criteria that assess reduction in geographic range (A), environmental degradation based on an abiotic variable (C) and...
quantitative analysis that estimates the probability of ecosystem collapse (E). None of these criteria fully consider the conservation implications of fragmentation and small patch size, which will have implications for habitat loss in the future.

Our new fragmentation measures are a first attempt in understanding and quantifying overall community vulnerability. We describe only how quantifying current patch contribution to overall extent in relation to original contribution can facilitate better understanding of ecosystem vulnerability. Although the proposed Gini metric enables a more complete understanding of the evolution of changes in the spatial structure of ecosystems, it is difficult to interpret if used alone without accompanying measures of fragmentation. For example, the absolute value of the Gini Index might be similar for two landscapes experiencing similar variation in patch inequality, but these landscapes might differ in the contribution of small patches (Table S6) as well as the extent, connectivity and spatial arrangement of habitat patches. Because we do not include data on the effect of habitat loss and fragmentation on species persistence, we suggest that our metrics be viewed as complementary to each other and to other existing fragmentation measures (Wang, Blanchet & Koper 2014; see Appendix S2 for an assessment of how measures compare). To fully describe the vulnerability of ecosystems to loss and fragmentation, we argue that it is necessary to apply both our measures and complementary assessments (e.g. connectivity, edge or perforation measures), in addition to understanding the biological meaning of these measures for species within those ecosystems (Riitters et al. 2000; Table S6).

Aside from general species–area hypotheses (Simberloff 1992), it is difficult to predict how most kinds of fragmentation might contribute to ecosystem vulnerability (Debinski & Holt 2000; Fahrig 2003). By accounting for the distribution of patches in the historical and the current study landscape, respectively, our measures improve on most existing fragmentation metrics that do not distinguish between natural and anthropogenic fragmentation. Although fragmentation clearly results in direct loss of some species and indirect loss of others due to vegetation removal or alteration, many species perform well in small isolated patches (Ryall & Fahrig 2006; Bowen et al. 2009). Many ecosystems naturally occur in small patches (Appendix S1), and therefore, the species within them have higher resilience to fragmentation than other communities. This variation in the sensitivity of biota to the species–area relationship across ecosystems and across taxa (Martensen, Pimentel & Metzger 2008) means that the patch size threshold cut-offs used to compare historical and current proportional contribution to remaining extent in this study (Fig. 4) will not necessarily generalize to other parts of the world. The appropriate scale at which to measure patch size vulnerability is the one at which the ecological response matches the landscape structure (Jackson & Fahrig 2012). Ideally, to better understand the importance of small patches, conceptual models of the interactions between vegetation community patch sizes, productivity and the requirements of the species within them should be developed (Villard & Metzger 2014). Because this varies across species and ecosystems, we suggest exploring a range of alternative threshold minimum patch areas, much like fish size restrictions are explored for sustaining recreational fisheries (Post et al. 2003).

For simplicity, we assumed that vegetation clearance was the only action affecting fragmentation and resulting patch size, and that patches were not connected if separated by more than 100 m (the resolution of the data set). Future studies could incorporate additional threatening processes such as infrastructure, which result in partial clearing and require knowledge of the impact on patch connectivity and persistence. Our approach does not attempt to quantify environmental degradation due to worsening vegetation condition, as condition data at a national level are rarely available, and detailed instructions for assessing this component (e.g. for the Red List of Ecosystems) have been prepared elsewhere (Keith et al. 2013). We used the Australian NVIS 1750 map to estimate historical (i.e. pre-clearing) conditions. This map has higher accuracy than some parts of the world because Australia has a relatively recent history of clearing. For countries or regions where detailed historical maps are not available, methods are now being developed based on predictive distribution modelling of historical ecosystem patterns (Ewers et al. 2013), geophysical mapping (Anderson & Ferree 2010; Sanderson, Segan & Watson 2015), or using genetics to determine historical biodiversity patterns in different areas (Boessenkool et al. 2014). Either way, making an assessment now is critical, as this can be updated over time in environmental accounts that record which ecosystems are worsening or improving.

The measures demonstrated in this study allow planners and researchers to assess how dependent ecosystems are on patches of different sizes. By exploring a range of patch size thresholds, planners and decision-makers can evaluate the vulnerability of communities in terms of cumulative loss of small vegetation remnants. Threshold limits to permissible clearing should vary across vegetation communities, dependent on the historical patchiness of the vegetation community as well as the contribution of small patches to the remaining extent. Our approach will improve our ability to evaluate overall change (e.g. through environmental accounts), explicitly consider and prioritize management actions to inform conservation planning (Margules & Pressey 2000) and evaluate the impact of potentially destructive activities such as development and extraction.

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Data accessibility

The Australian Government National Vegetation Information System (sensis Version 4.1) is freely available for download (http://www.environment.gov.au/).


References


Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details of loss and fragmentation analyses for all vegetation communities.

Appendix S2. Metric comparisons and supporting code.

Appendix S3. Characterizing community change.

Fig. S1. Percentage change in the overall extent, and number of patches, of the 75 broad vegetation communities (as defined by NVIS) in Australia.

Fig. S2. Relative change in vegetation community extent versus (a) a traditional edge metric measuring fragmentation \( F = (A_0/A_1)/(E_0/E_1)^2 \) and (b) total change in contribution of patches <5000 ha.

Table S1. Results of patch threshold metrics and Gini coefficient for all 75 NVIS vegetation communities.

Table S2. Ranks of the 75 vegetation communities with respect to the three measures of loss, fragmentation and equality.

Table S3. Size of the patch at varying thresholds of cumulative extent for all 84 vegetation communities based on current conditions.

Table S4. Size of the patch at varying thresholds of cumulative extent for all 75 vegetation communities based on 1750 conditions.

Table S5. Results of Kolmogorov–Smirnov tests to determine if the distributions of patch sizes for all 75 vegetation communities based on pre-1750 conditions differ from the current patch size distributions of those communities.

Table S6. Characteristics of loss and fragmentation of vegetation communities in Australia.