

A systematic review reveals changes in where and how we have studied habitat loss and fragmentation over 20 years

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38 **Abstract**

39 Habitat loss and fragmentation are global threats to biodiversity and major research
40 topics in ecology and conservation biology. We conducted a systematic review to
41 assess *where* – the geographic locations and habitat types - and *how* – the study
42 designs, conceptual underpinnings, landscape metrics and biodiversity measures -
43 scientists have studied fragmentation over the last two decades. We sampled papers
44 from 1994 to 2016 and used regression modelling to explore changes in fragmentation
45 research over time. Habitat loss and fragmentation studies are geographically and
46 taxonomically biased. Almost 85% of studies were conducted in America and Europe,
47 with temperate forests and birds the most studied groups. Most studies use a binary
48 conceptual model of landscapes (habitat versus non-habitat) and static measures of
49 biodiversity. However, research on fragmentation is slowly shifting from a focus on
50 coarse patterns to more nuanced representations of biodiversity and landscapes that
51 better represent ecological processes. For example, empirical research based on
52 gradient or continuum models, that offer new insights into landscape complexity and
53 species-specific responses to habitat fragmentation, are increasing in prevalence. We
54 recommend that fragmentation research focuses on developing knowledge on
55 underlying mechanisms and processes of how species respond to landscape changes,
56 and that fragmentation studies be conducted in the full range of habitats currently
57 experiencing high rates of landscape modification. This is crucial if we are to
58 understand relationships between biodiversity and ecosystems and to develop
59 effective management strategies in fragmented landscapes.

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62 **Key words:** biodiversity, connectivity, continuum model, global change, landscape
63 mosaic, taxonomic bias

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79 **Introduction**

80 Over the last century, habitat loss and fragmentation have been the main
81 drivers of biodiversity change in terrestrial ecosystems (Laurance et al. 2012;
82 Newbold et al. 2015). A recent synthesis of 35 years of fragmentation experiments
83 across multiple spatial scales revealed that habitat loss and fragmentation has reduced
84 biodiversity by 13 to 75% in five continents, and more than 70% of the world's
85 remaining forests are now in close proximity to modified environments (Haddad et al.
86 2015). Rapid habitat loss and fragmentation is particularly concerning in biodiversity
87 hotspots such as tropical forests and temperate grasslands, and these trends are likely
88 to continue (Millennium Ecosystem Assessment 2005; Gardner et al. 2009).

89 Given its important role in global change, habitat loss and fragmentation
90 continues to be an important research topic in ecology and conservation biology
91 (Tscharntke et al. 2012; Driscoll et al. 2013). The literature on fragmented landscapes
92 is vast and growing: a search of “habitat fragmentation” in Thomson Reuters Web of
93 Science (environmental science ecology research area) from 1980 yielded over 3,800
94 published papers, or more than 10% of total ecology papers available. Rapid progress
95 has been made in habitat loss and fragmentation research in only a few decades,
96 and the results of this work have particularly influenced applied problems such as
97 design of nature reserves, and management of agricultural landscapes, urban areas and
98 forest harvesting (Lindenmayer et al. 2006). However, identifying and quantifying
99 general patterns and processes in this large body of literature remains difficult. The
100 fragmentation literature encompasses many experimental designs and methods
101 (Bennett et al. 2006), choices of landscape measurements (Kool et al. 2013),
102 landscape classifications (Lindenmayer and Fischer 2007), and ways of representing
103 biodiversity (Ewers and Didham 2006).

104 To synthesise habitat loss and fragmentation research, much effort has been
105 applied to the development of the theoretical concepts and landscape models that
106 underpin our understanding of these processes (Fischer and Lindenmayer 2007; Price
107 et al. 2009; Laurance et al. 2011b; Didham et al. 2012). A simple and influential
108 conceptual model of habitat fragmentation is based on island biogeography theory
109 (MacArthur and Wilson 1967). This binary view of habitat and non-habitat (e.g.
110 Diamond 1975) led to the development of more complex ways of classifying
111 landscapes such as the patch-corridor-matrix model (Forman and Godron 1981), the
112 landscape mosaic model (Wiens 1995), and, more recently, models that recognise
113 habitat gradients and continuums (McIntyre and Hobbs 1999; Manning et al. 2004;
114 McGarigal and Cushman 2005; Fischer and Lindenmayer 2006). A shift from a simple
115 binary model to more complex mosaic and continuum models requires new ways of
116 measuring landscape patterns. We predict that methods to measure landscapes have
117 kept up with the development of these conceptual models. However, which methods
118 have developed and how fast they have developed remains unclear.

119 Numerous metrics have been developed to measure landscape composition
120 (identity and characteristics of landscape elements), configuration (spatial
121 arrangement of landscape elements), and connectivity (the ease with which organisms
122 move through the landscape) (Hanski 1994; Hargis et al. 1998; Tischendorf and
123 Fahrig 2000). A range of tools and software have also been developed to assist this
124 quantification (e.g. “FRAGSTATS” (McGarigal et al. 2002), “Circuitscape” (Shah and
125 McRae 2008), and “Conefor” (Saura and Torne 2009). Landscape metrics have been
126 used to describe habitat loss and fragmentation at a range of different spatial scales

127 from patches to whole landscapes (Bennett et al. 2006). Despite development in
128 experimental design and landscape measures, the use of different approaches has led
129 to very different conclusions regarding the magnitude and direction of fragmentation
130 effects (Fahrig 2003). There is little consensus regarding which aspects of landscape
131 structure and composition should be studied for describing biodiversity responses to
132 fragmentation (Ewers et al. 2010; Fahrig 2015; Hanski 2015). Several narrative
133 reviews have highlighted the range of landscape metrics available (Kool et al. 2013),
134 and alternative ways to study landscape change (Brennan et al. 2002; Bennett et al.
135 2006; Fahrig et al. 2011), but few studies have quantified how the use of metrics and
136 alternative study designs is changing over time.

137 Another issue relates to taxonomic and geographical biases in ecology. Ideally,
138 fragmentation research should comprehensively cover a range of geographical regions
139 and taxonomic groups to provide robust data that support effective conservation
140 policies and actions. We predict that, as in conservation biology and ecology more
141 broadly (Trimble and van Aarde 2012; Burgman et al. 2015), our knowledge of how
142 habitat fragmentation and landscape patterns affect biota is biased towards large
143 faunas in temperate regions. These forms of bias will be particularly problematic if
144 fragmentation affects geographic regions and taxa in different ways (Thornton et al.
145 2011).

146 Systematic review is an important tool for evaluating conservation evidence
147 and supporting environmental decision making (Pullin and Knight 2009). It is also
148 useful for identifying knowledge gaps and methodological inconsistencies across
149 disciplines and to focus research priorities (Pullin and Knight 2009; Mallett et al.
150 2012; Haddaway and Pullin 2014). To date, researchers have systematically reviewed
151 habitat loss and fragmentation studies for specific sections of the literature including
152 experimental manipulations of habitat fragmentation (Debinski and Holt 2000;
153 McGarigal and Cushman 2002), the interactions between climate and habitat loss
154 (Mantyka-Pringle et al. 2012), the use of landscape spatial metrics (Uuemaa et al.
155 2013), dispersal research for landscape planning and restoration (Driscoll et al. 2014),
156 and within particular habitat types (e.g. tropical forests, Deikumah et al. 2014).
157 However, systematic analyses of the broader literature on habitat loss and
158 fragmentation, including a range of ecosystems, study types and measures, are rare
159 and few have examined how the literature has changed over time.

160 In this paper, we systematically review the development of habitat loss and
161 fragmentation research over more than 20 years to identify where and how research
162 has been undertaken and in what way it has changed over time. Specifically, we asked:
163 1) What conceptual models have been used in fragmentation studies, and how have
164 the use of these models changed over time? 2) How have biodiversity responses to
165 landscape modification been measured, and how have these measures changed over
166 time? 3) What landscape metrics have been used to describe habitat loss and
167 fragmentation, and how have their use changed over time? and 4) How are these
168 studies distributed across regions, habitat types and taxa?

169

170 **Methods**

171 To examine trends in habitat loss and fragmentation studies, we undertook a
172 systematic review of the literature. For each paper in our sample we recorded
173 information on the study design, geographic region and taxa considered, and the

174 underlying conceptual model, the biodiversity responses measured, and the landscape
175 metrics used. We then modelled how these attributes have changed over time using
176 logistic regression.

177

178 *Systematic literature search*

179 We first conducted a search of all peer-reviewed ecological articles indexed by
180 the Thomson Reuters Web of Science Core Collection (Sci-Expanded) from 1 January
181 1980 to 31 June 2016 using the keyword “ecology”. We initially searched papers
182 starting from the 1980’s because this was when landscape ecology clearly emerged as
183 a unique scientific discipline (Wiens 2007). We refined the search by type of
184 document (article), research area (environmental science-ecology), and language
185 (English), which resulted in 39,045 articles. We conducted another search using
186 keywords that are related to habitat fragmentation and landscape change: "habitat
187 fragmentation" or "forest fragmentation" or “grassland fragmentation” or “woodland
188 fragmentation” or “savanna fragmentation” or “shrubland fragmentation” or “tundra
189 fragmentation” or “heathland fragmentation” or “xeric shrubland fragmentation” or
190 “scrub fragmentation” or “desert fragmentation” or “mangrove fragmentation” or
191 “river fragmentation” or "landscape fragmentation" or "habitat connectivity" or
192 "landscape connectivity" or "patch connectivity" or "patch isolation" or "habitat
193 isolation". This search resulted in a subset of 6,341 articles from the broader sample.
194 Using both searches, we then calculated the proportion of fragmentation studies
195 within ecological science for each year to examine the prevalence of fragmentation
196 studies in the ecological literature (supplementary material S1, Fig. A1).

197 A check of additional search terms including “fragment*”, “isolat*” and
198 “connect*” in Web of Science increased the total number of papers found by
199 approximately 10%. Because adding these new terms added only a relatively small
200 number of additional papers we present the results from our original search in the
201 present paper.

202 As the number of fragmentation papers increased substantially in the
203 beginning of the 1990’s, we decided to limit our systematic review to 6,252 papers
204 that were published between 1994 and 2016 (23 years). This guaranteed that we
205 sampled enough papers in each year to develop statistical models of changes in the
206 literature. We randomly selected 20 articles from each of the 23 years (460 in total).
207 We screened the selected articles and excluded articles that did not measure habitat
208 loss and fragmentation or did not examine fragmentation effects on biodiversity. We
209 also excluded articles that did not present empirical or simulated data (including
210 review papers and opinion papers). The remaining 302 focal articles were then
211 reviewed in full for data extraction (Fig. 1). Finally, we calculated the standard error
212 of the sample population for each year to ensure we had a large enough sample size to
213 complete our analysis (following Sokal and Rohlf (1995)). The number of papers
214 analysed each year is presented in Table A2.

215

216 *Classification of the literature*

217 We categorised each of the focal articles by a range of attributes including
218 study design (type of study, source of data, unit of inference), conceptual model of
219 habitat loss and fragmentation, type of landscape metric, type of biotic response,
220 geographic location, biome, focal organism, species conservation status, and highest

221 level of biological organisation (Table A3). For attributes of study design, conceptual
222 model, and highest organisational level, each study was allocated to a single category.
223 For other attributes, studies could be allocated to multiple categories. We examined
224 the reliability of classification by having two of the authors (DF and LTK) read the
225 same subsample of papers and checking that the categorisation of papers matched.

226

227 *Research Topic*

228 We examined trends in the number of published papers with respect to each
229 study attribute. To analyse the trends, we first calculated the proportion of studies in
230 each category of attribute for each calendar year. We then conducted a logistic
231 regression to calculate the rate of change in the proportion of studies per year for each
232 category:

233

$$y(i) = \frac{e^{(\beta_0 + \beta_1 x_i)}}{1 + e^{(\beta_0 + \beta_1 x_i)}}$$

234

235 where $y(i)$ is the proportion of studies in year i , β_0 is the model intercept, β_1 is the rate
236 of change, and x_i is year i . We first specified a binomial distribution for each model,
237 and, where the dispersion of the residuals suggested over- or under-dispersion, we
238 used quasibinomial regression and beta regression, respectively (Hilbe 2009).

239 We also calculated the predicted number of all fragmentation papers in each
240 category based on the logistic model and the difference in predicted number of papers
241 between years 2016 and 1994 to estimate changes in number of papers in 23 years. To
242 do this, we first computed the predicted number of papers for each category from the
243 fitted values of logistic regression:

244

$$\hat{p}(i) = \frac{e^{(\beta_0 + \beta_1 x_i)}}{1 + e^{(\beta_0 + \beta_1 x_i)}} \times \text{number of fragmentation papers in year } i$$

245

246 We then calculated the changes in 23 years as:

247

$$248 \Delta \hat{p} = \hat{p}(2016) - \hat{p}(1994)$$

249

250 These changes represented the predicted number of fragmentation papers
251 published between 1994 and 2016, with respect to each topic. We used package
252 'MASS' (Venables and Ripley 2002) in R version 3.2.2 for all logistic regression
253 analyses (additional details in supplementary material S4, Table A4). We also
254 analysed potential interactions in the use of conceptual models across different habitat
255 types and regions using chi-square tests in the R Base Package.

256

257 **Results**

258 The keyword search for the systematic review returned a total of 6,252 articles
259 published between 1994 and 2016. The 460 sampled articles came from 87 different
260 scientific journals. *Biological Conservation* and *Conservation Biology* were the most
261 prevalent journals (9.8% and 7.8%, respectively). *Landscape Ecology*, *Biodiversity*
262 *and Conservation* and *Ecological Applications* rounded out the top five journals
263 (6.7%, 5.2% and 4.8% of articles, respectively). A full list of journals is presented in
264 Table A5.

265

266 *Study design*

267 Of the 302 focal articles reviewed, the majority reported new data (90.4%),
268 while the rest used existing data sets (6.0%) or simulated data (3.6%). Most of the
269 articles used natural experiments (76.5%) and field experiments (15.9%). Few studies
270 were solely based on simulations (6.6%) or laboratory experiments (1%).

271 Almost half of the studies measured fragmentation using a focal patch
272 approach (47%), that takes into account the effects of the surrounding landscape on
273 species responses to habitat loss and fragmentation. A similar number of studies used
274 individual patches as the unit of inference (45.7%). Only 7.3% of the studies used a
275 “whole-of-landscape” approach where both the response and predictor variables were
276 measured at a landscape-level. Despite their lower prevalence, landscape-level studies
277 have increased as a proportion over the past 23 years, whereas patch-level studies
278 have decreased (Fig. 2).

279

280 *Conceptual model*

281 Studies more commonly conformed to a binary conceptual model (73.5%)
282 than a mosaic (15.9%) or continuum model (10.6%). However, over time the use of
283 the binary model decreased as a proportion of total fragmentation studies (Fig. 3). By
284 contrast, the continuum and mosaic models are being increasingly used (Fig. 3). There
285 was no difference in the use of conceptual model among habitat types ($\chi^2_{(7, N=293)} =$
286 $8.06, p > 0.05$) or regions ($\chi^2_{(5, N=293)} = 8.66, p > 0.05$) (Tables A6 and A7).

287

288 *Species response*

289 More than half (61.3%) of the studies measured the effect of habitat
290 fragmentation on species distributions (i.e. biodiversity measured as abundance,
291 occurrence or changes in range size) (Fig. 4). Measures of diversity and population
292 dynamics were also commonly used (34.4% and 28.1%, respectively). Other response
293 variables, such as movement (13.2%), genetics (12.9%), morphology/physiology
294 (11.9%) and biotic interactions (11.3%) were less common measurements. Despite
295 their lower percentages, studies examining movement and morphology/physiology are
296 becoming more common (Fig. 4). Although there was a decrease in the proportion of
297 papers that focused on species distributions, the total number of studies that examined
298 this response increased more than any other measures over 23 years.

299

300 *Landscape metric*

301 Area metrics and isolation/proximity metrics were those most commonly used
302 in our sample of the fragmentation literature (48% and 42.4%, respectively). The use
303 of area metrics has significantly decreased over time, whereas isolation/proximity
304 metrics have increased moderately (Fig. 5). Measures including core area,
305 disturbance/succession, contrast, and patch type decreased in prevalence, while least
306 cost models, graph theory, and incidence function model have started to be used more
307 frequently. Despite declining proportional rates of use, the absolute number of studies
308 that used measures of patch area and habitat amount was still growing (Fig. 5).

309

310 *Geographic location and habitat type*

311 We identified several locational biases (Fig. 1). Most articles examined
312 fragmentation in regions with extensive temperate vegetation such as Northern
313 America (36.8%), Australia/New Zealand (12.9%), Western Europe (12.3%) and
314 Northern Europe (7.6%) (Fig. 6). A smaller percentage of studies were conducted in
315 regions containing large areas of tropical vegetation such as South America (13.2%)
316 and Central America (7.9%). Africa, most parts of Asia, and southern and eastern parts
317 of Europe were the least represented regions in our sample, and none of the random
318 subset of 302 papers reviewed described studies conducted in the Caribbean, Central
319 Asia, Polynesia, Micronesia or Northern Africa. Nevertheless, over the past 23 years,
320 the absolute number of studies conducted in Asia, Africa and South America was
321 increasing (Fig. 6).

322 Fragmentation studies were also biased by habitat, with most studies
323 conducted in temperate ecosystems. More studies were conducted in temperate forests
324 (43%) than tropical and subtropical forests (21.5%), despite the greater extent of
325 tropical and subtropical forests. The number of papers about tropical and subtropical
326 forests increased substantially over time, as did the number of papers focusing on
327 freshwater ecosystems (Fig. A8). In both temperate and tropical areas, grassland
328 ecosystems received less attention compared to forests, however grassland-focused
329 studies in tropical systems increased over time. Tropical grasslands/savannas,
330 deserts/xeric shrublands, and boreal forests all cover relatively large areas (Fig. A9),
331 but were among the least represented habitats (4.3%, 4% and 3.6% of studies,
332 respectively) (Fig. A8).

333

334 *Taxonomic group, status and organisational level*

335 Few taxonomic groups were well represented (Fig. 7). Birds and mammals
336 were most commonly studied (27.5% and 22.8% of studies, respectively). Other
337 vertebrate taxa such as amphibians, reptiles and fishes were represented infrequently
338 (5.6%, 4.6%, and 2.3% of studies, respectively). Vascular plants were represented in
339 nearly a quarter of sampled studies (24.2%). Of the 62 papers studying invertebrates,
340 most studied insects (49 papers, 16.2% of focal studies). Only molluscs were
341 represented in the studies of non-arthropod invertebrate taxa (1.7%).

342 Of the 155 papers where species status could be identified, studies on non-
343 threatened species (57.4%) were far more common than those of threatened (16.1%).
344 Most studies were conducted at assemblage level (43.4%), or single (individual)
345 species level (40.1%), whereas few studies analysed the effects of fragmentation at
346 community and ecosystem levels (13.2% and 2.3%, respectively). There was an

347 increasing trend in single species studies, while studies of multiple species decreased
348 or were static (Fig. 7).

349

350 **Discussion**

351 Habitat loss and fragmentation have been a major research focus for ecologists
352 and conservation biologists over the past 23 years, constituting as much as 20% of all
353 studies in ecology and environmental research in some years. We present evidence for
354 preferential selection of conceptual models used to define fragmentation, the
355 biodiversity responses examined, and the landscape metrics used for measuring
356 fragmentation. Overall, our systematic review shows that research on habitat loss and
357 fragmentation is shifting from a focus on coarse patterns to more nuanced
358 representations of biodiversity and landscapes that better represent ecological
359 processes, although at slower rate than we expected. These new insights into how
360 fragmentation research is changing over time were only possible through systematic
361 review spanning more than two decades.

362

363 *Simple conceptual models remained popular, but the use of more complex models*
364 *increased*

365 As predicted, there was a strong preference for using a binary model of
366 landscape classification in fragmentation research. The binary model was among the
367 first conceptual models developed to describe patterns of landscape change (Haila
368 2002), and it is relatively easy to implement because of its simple representation of
369 landscapes and minimal data requirements. The binary model is well suited for
370 landscapes that are dominated by clearly defined boundaries, units or patches.
371 However, many landscapes consist of continuous gradients or mosaics of different
372 elements, and the binary model can oversimplify habitat fragmentation (Fischer and
373 Lindenmayer 2006). For example, a pixel-by-pixel comparison of a binary and a
374 continuous map showed that around 87% of the habitat quality information in the
375 continuous map could not be accounted for by the binary map (Cushman et al. 2010).

376 In one of few studies to empirically test the use of different landscape
377 conceptual models, Price et al. (2009) showed that the usefulness of different models
378 varied among species, depending on species associations with different landscape
379 elements. Despite the large number of studies using binary models, studies that
380 represent landscapes as continuums are increasing at a greater rate. Technological
381 advances in remote sensing and data analysis, as well as advances in our
382 understanding of landscape connectivity, have assisted the shift towards more
383 complex landscape models by enabling researchers to collect and analyse more
384 complex data on habitat fragmentation (Duputie et al. 2014).

385 In summary, discrete models can provide useful representations of landscapes
386 with clear spatial boundaries that have been demonstrably linked to species
387 distributions (Dunn and Majer 2007). Gradient models, by contrast, can provide
388 insight on species responses in landscapes with less marked transitional boundaries
389 (Bruton et al. 2015). There is a trade-off between information content and data
390 requirements across different fragmentation models. The choice of conceptual model
391 should be determined by the research question asked, the ecosystem studied, the scale
392 of observation, and the availability of data and tools needed for the analysis.

393

394 *From patches to landscapes*

395 The majority of studies measured fragmentation at the patch or focal patch
396 level. Although only 7% of the studies used a “whole-of-landscape” approach – where
397 both the response and predictor variables were measured at a landscape-level (Bennett
398 et al. 2006) – this landscape study design has become more common over the past 23
399 years. A whole-of-landscape approach has provided new insights into the relative
400 influence of landscape composition and configuration on biodiversity in fragmented
401 landscapes (Fahrig et al. 2011) – with most empirical studies to-date showing stronger
402 effects of landscape composition, rather than configuration, on biodiversity (Radford
403 and Bennett 2007; Haslem and Bennett 2008; Mortelliti et al. 2011).

404

405 *Pattern-based measures of biotic responses were preferred*

406 Preferences in the underlying fragmentation model were reflected in the
407 choice of biological responses and landscape metrics used in the studies. Overall,
408 static counts of biodiversity such as abundance and species richness were the most
409 common response variables. These measurements are commonly used because they
410 are easy to calculate and interpret, and because they often explain and predict species
411 responses to habitat fragmentation (Colwell 2009). However, as these measures
412 emphasise pattern, they may provide an inadequate representation of some biological
413 processes (Turner 2006). On the other hand, process-based measures such as
414 population dynamics, biotic interactions and dispersal are typically more difficult to
415 measure, requiring extensive measurements and pose more methodological challenges.
416 This may explain the reduced attention given to these measures in fragmentation
417 studies. The complexity of these measures, however, comes with the advantage of
418 more realistic prediction of the interactions between species distribution and
419 characteristics of particular landscapes (Wiegand et al. 2005).

420 Studies of animal movement are increasing in prevalence, but process-based
421 measurements relating to population dynamics are decreasing in prevalence. The
422 growing interest in movement studies that we identified is likely due to recent
423 advances in technology used for observing species dispersal, such as radio, satellite
424 and radar tracking (Nathan et al. 2003; Bridge et al. 2011), as well as the rapid
425 development of methods for species distribution modelling (Bocedi et al. 2014).
426 Studies that incorporate population dynamics require substantial field data to calculate
427 and parameterise demographic models (Baguette 2004).

428

429 *Pattern-based landscape metrics are common, but there is an increasing trend for*
430 *process-based metrics*

431 The use of relatively simple landscape measurements such as area and distance
432 for quantifying landscape pattern remain popular in fragmentation research and can be
433 suitable for making conservation decisions (Calabrese and Fagan 2004). However, we
434 identified an increasing trend in the use of metrics that aim to capture a greater range
435 of the landscape elements that determine species responses to habitat loss and
436 fragmentation. These metrics, including incidence function models, least cost models
437 and graph theory, can incorporate ecological processes such as movement and
438 population dynamics in their calculation (Prugh 2009). By combining physical

439 attributes of the landscape with the species information, these metrics offer the
440 potential to quantify how habitat loss and fragmentation influence animal movement,
441 connectivity and landscape resistance (Shah and McRae 2008). The advantages of
442 using metrics that incorporate multiple landscape elements and ecological processes,
443 however, come at a cost of greater complexity, as they can be difficult to use and
444 require labour-intensive data collection. We hypothesise that this explains the lower
445 proportion of process-based metrics in our systematic review.

446

447 *Fragmentation studies were geographically and taxonomically biased*

448 The majority of fragmentation research has been carried out in relatively
449 wealthy countries. However, most natural ecosystems and biodiversity hotspots are
450 located in developing parts of Asia, Africa and South America that are currently
451 experiencing the most rapid change (Myers et al. 2000; Smith et al. 2003; Fearnside
452 2005; Newbold et al. 2015; Fig. A9). The relatively small number of fragmentation
453 studies conducted in these regions is likely due to limited financial support,
454 inadequate infrastructure and political instability (Holmgren and Schnitzer 2004).
455 Lack of quantitative ecological training in developing countries, and language barriers,
456 have also potentially impeded the amount and quality of research in particular
457 geographic locations (Griffiths and Dos Santos 2012). A recent review revealed that
458 only 7% of ecology and biodiversity conservation submissions, in one international
459 journal, came from Africa, Asia, Central and South America, whereas submission
460 from North America, Oceania and Europe were three times as common (Burgman et
461 al. 2015).

462 Geographic and taxonomic biases are acknowledged in ecology and
463 conservation biology. Nevertheless, Cronin et al. (2014), in a review of the broader
464 wildlife conservation literature, reported that there has been some increase in research
465 undertaken in tropical regions such as Central America, South America, Southern Asia,
466 and South-eastern Asia over the past 20 years. This is consistent with our observations
467 for the fragmentation literature. Notable habitat loss and fragmentation studies include
468 the Borneo Futures Project in Indonesian and Malaysian Borneo (Wilson et al. 2010),
469 the Biological Dynamics of Forest Fragments Project in Brazil (Laurance et al. 2011a),
470 and the Stability of Altered Forest Ecosystem (SAFE) Project in Malaysian Borneo
471 (Ewers et al. 2011).

472 We only reviewed papers written in English and this might have biased the
473 geographic distribution of the studies we sampled. There is a need to better integrate
474 studies published in languages other than English with the broader international
475 literature. To facilitate better integration of research from under-represented countries,
476 useful actions include enhancing training of local conservation biologists, community-
477 based organisations and field staff through higher-level education, and promoting
478 partnerships and research visits among local researchers and international research
479 institutions.

480 Compared to forests, grasslands and aquatic habitats have received much less
481 attention in fragmentation studies. This could reflect the focus of early landscape
482 ecology studies on forest ecosystems. For example, a search of the phrase “grassland
483 fragmentation” resulted in less than 2% of the hits returned for “forest fragmentation”.
484 In a recent review, Wilson et al. (2012) found that grasslands harbour more plant
485 species at smaller spatial grains (less than 50 m² quadrats) compared to tropical

486 rainforests. Moreover, grasslands are generally considered to be more vulnerable than
487 forests to habitat destruction because they are easy to cultivate and their location often
488 makes them vulnerable to overgrazing and urbanisation (Dauber et al. 2006; Newbold
489 et al. 2016). We recommend fragmentation studies be conducted in the full range of
490 habitats currently experiencing high rates of landscape modification because threats to
491 biodiversity are not restricted to forests.

492 Fragmentation research has been dominated by work on birds, mammals and
493 vascular plants, presumably because larger animals and plants are valued by people,
494 are a priority for most conservation managers and are relatively cost-effective to study.
495 However, there is a risk that such biases could limit understanding of relationships
496 between understudied taxa and their environments, and thus could potentially hamper
497 effective conservation efforts for multiple taxa. We also found that there were more
498 studies conducted for single taxa and non-threatened species. Based on the IUCN Red
499 List, 26.7% of species are categorised as threatened (critically endangered,
500 endangered, vulnerable, and near threatened), 56.7% as least concern and 15.2% as
501 data deficient. Thus, even when compared to the proportion of threatened species
502 globally, our systematic review shows that there is a lack of studies on how habitat
503 loss and fragmentation influence threatened species. The increase in the number of
504 single-species studies suggests that there is growing interest in obtaining a more
505 detailed, mechanistic understanding of habitat fragmentation.

506

507 *Better understanding habitat loss and fragmentation*

508 Rapid progress has been made in fragmentation research in the past two
509 decades. Our study shows that pattern-based research is still dominating the
510 fragmentation literature, despite calls for change (Fischer and Lindenmayer 2006;
511 Didham et al. 2012). This can be seen from the choice of response variable,
512 conceptual model and landscape metrics used for conducting the research that are still
513 based more commonly on pattern than ecological processes.

514 A moderate increase in process-based research reflects changes in the way we
515 perceive and manage landscapes. For example, a shift towards appreciating
516 landscapes as gradients or continuums has led to a renewed focus on the role of
517 'matrix' habitat in agricultural landscapes (Driscoll et al. 2013). In turn, this has
518 influenced government investment and on-ground management by placing a greater
519 emphasis on landscape wide and off-reserve (or private land) conservation strategies
520 that aim to increase habitat quality and improve connectivity to reduce negative
521 fragmentation effects (Chan and Daily 2008; Arponen et al. 2013; Duarte et al. 2014).

522 Different conceptual models, study designs and landscape measures have
523 different strengths and limitations (Table A10), and the approach used for a given
524 study will depend on the study objectives and the ecological and landscape
525 management contexts. Although understanding pattern is important in ecological
526 research, understanding the mechanisms and underlying processes of how species
527 respond to landscape changes is crucial if we are to understand relationships between
528 biodiversity and ecosystems, a necessary precursor to developing effective
529 management strategies in fragmented landscapes. As both single-species and
530 ecosystem studies have their own strengths and limitations, we recommend a
531 combination of both approaches in order to develop effective management strategies

532 and increase the potential for successful conservation outcomes in fragmented
533 landscapes (see also Lindenmayer et al. (2007)).

534 The geographical and taxonomic biases that we found in the literature limit
535 our understanding of biodiversity and ecosystem function in different fragmented
536 landscapes. Knowledge gaps caused by these biases could further limit the
537 development and the implementation of effective strategies for managing habitat loss
538 and fragmentation in areas where the crisis is greatest. The increasing number of
539 studies conducted in tropical developing countries means that the focus of attention is
540 currently shifting to where conservation is needed the most. We suggest that more
541 attention be given to further promote and facilitate research in these understudied
542 regions to improve empirical evidence of biodiversity persistence and appropriate
543 habitat management in these landscapes.

544

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549

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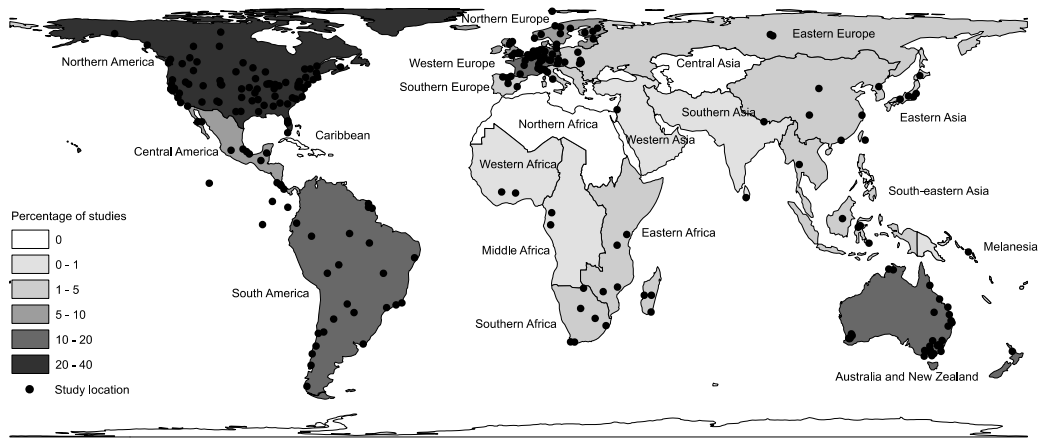
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781 **Figures**



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783 **Fig. 1.** The location of the 302 habitat loss and fragmentation studies data were
 784 extracted from. Shading highlights the percentage of studies by geographic region.

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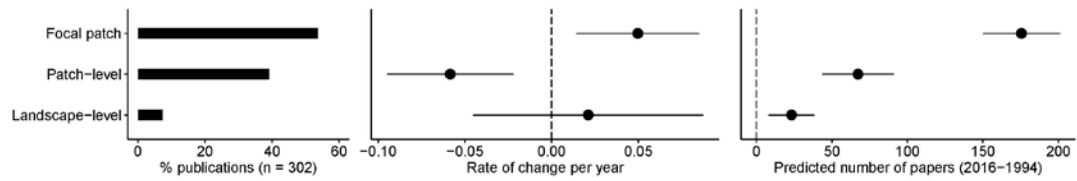
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807 **Fig. 2.** Unit of inference. Percentage of sample publications (n=302), rate of change in
 808 proportion of studies per year, and the predicted number of fragmentation papers in
 809 2016 compared to 1994 for each category of unit of inference. Error bars represented
 810 the 95% confidence interval from a logistic regression.

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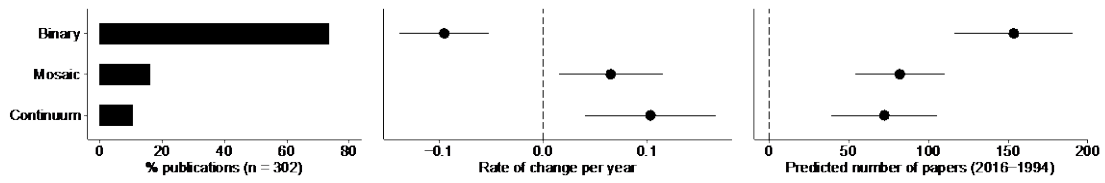
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839 **Fig. 3.** Conceptual model. Percentage of sample publications (n=302), rate of change
 840 in proportion of studies per year, and the predicted number of fragmentation papers in
 841 2016 compared to 1994 for each category of conceptual model. Error bars represented
 842 the 95% confidence interval from a logistic regression.

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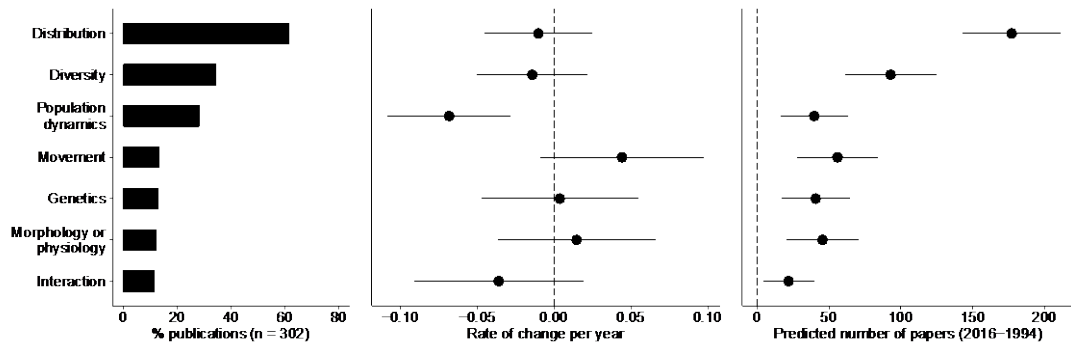
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872 **Fig. 4.** Biodiversity response. Percentage of sample publications (n=302), rate of
 873 change in proportion of studies per year, and the predicted number of fragmentation
 874 papers in 2016 compared to 1994 for each category of biodiversity response measured
 875 Error bars represented the 95% confidence interval from a logistic regression.

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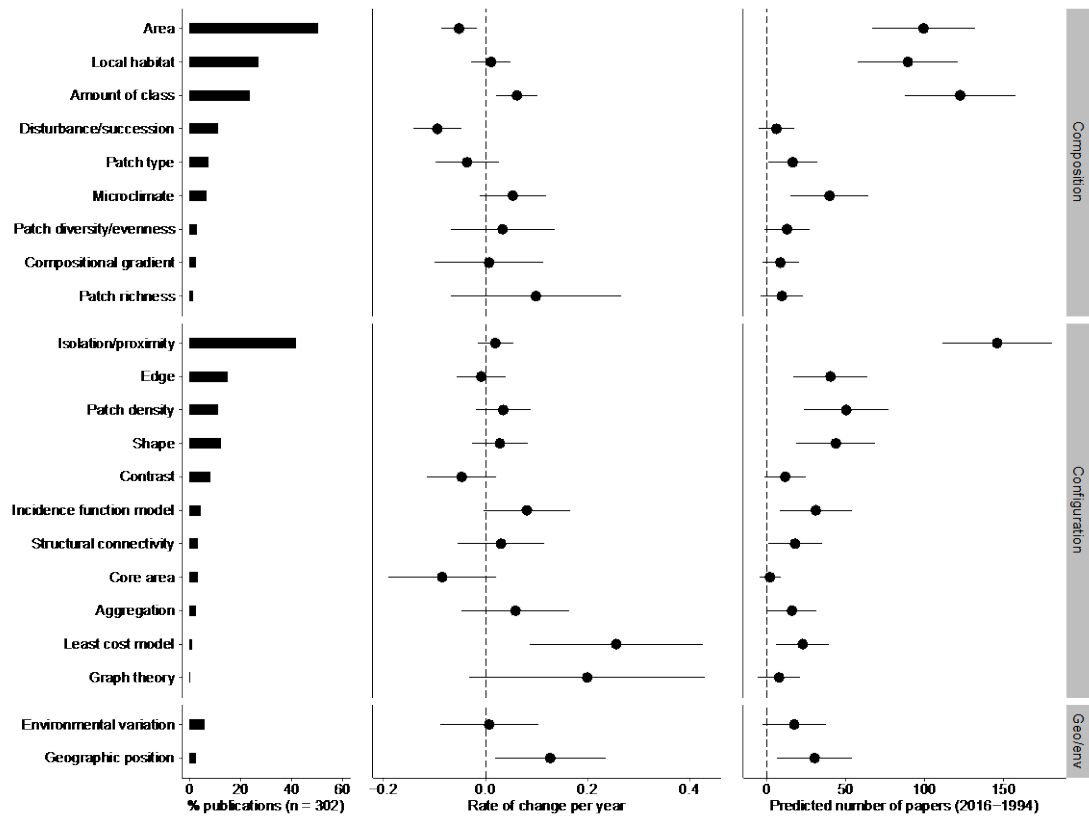
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902 **Fig. 5.** Landscape metric. Percentage of sample publications (n=302), rate of change
 903 in proportion of studies per year, and the predicted number of fragmentation papers in
 904 2016 compared to 1994 for each category of landscape metric used. Error bars
 905 represented the 95% confidence interval from a logistic regression.

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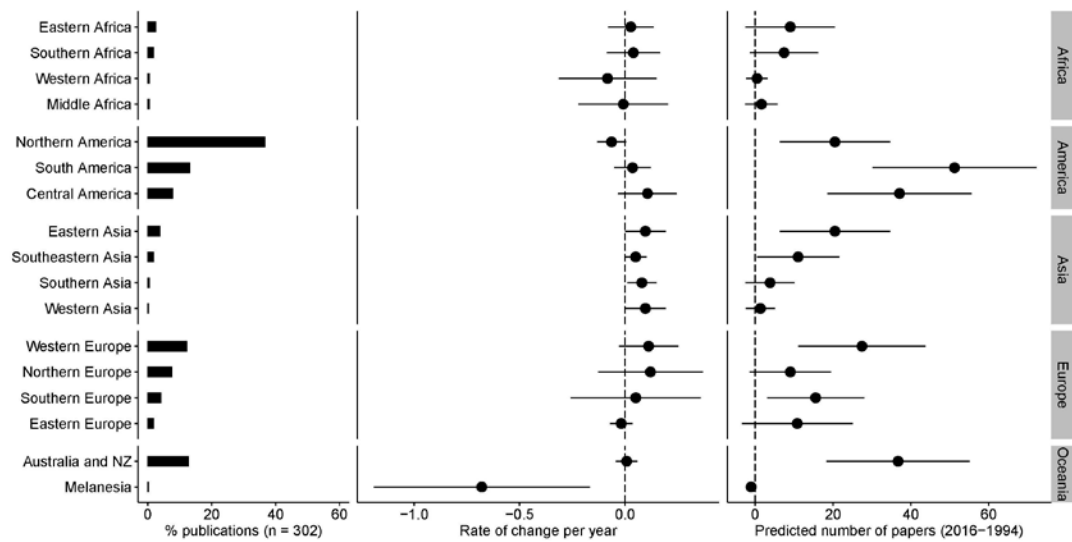
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923 **Fig. 6.** Geographic location. Percentage of sample publications (n=302), rate of
 924 change in proportion of studies per year, and the predicted number of fragmentation
 925 papers in 2016 compared to 1994 in each geographic location. Error bars represented
 926 the 95% confidence interval from a logistic regression.

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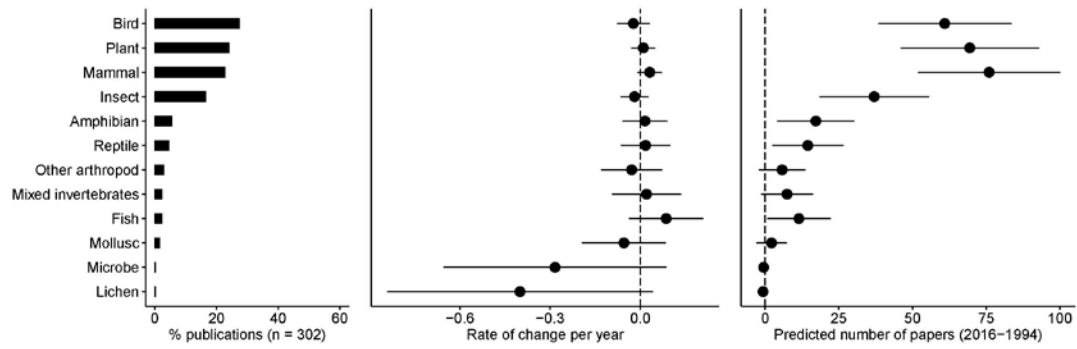
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948 **Fig. 7.** Focal organism. Percentage of all publications (n=302), rate of change in
 949 proportion of studies per year, and the predicted number of fragmentation papers in
 950 2016 compared to 1994 for each category of taxa. Error bars represented the 95%
 951 confidence interval from a logistic regression.