

1 **Reframing landscape fragmentation's effects on ecosystem services**

2

3 Matthew G.E. Mitchell¹, Andrés F. Suarez Castro¹, Maria Martinez-Harms²,

4 Martine Maron¹, Clive McAlpine¹, Kevin J. Gaston³, Kasper Johansen¹, Jonathan

5 Rhodes^{1,2}

6

7 ¹ School of Geography, Planning and Environmental Management, The University
8 of Queensland, Brisbane, QLD 4072, Australia

9 ² Australian Research Council Centre of Excellence for Environmental Decisions,
10 School of Biological Sciences, The University of Queensland, Brisbane, QLD
11 4072, Australia

12 ³ Environment and Sustainability Institute, University of Exeter, Penryn,
13 Cornwall TR10 9FE, United Kingdom

14 **Abstract**

15 Landscape structure and fragmentation have important effects on ecosystem
16 services, with a common assumption that fragmentation reduces service
17 provision. This is based on fragmentation's expected effects on ecosystem
18 service supply, but ignores how fragmentation influences the flow of services to
19 people. Here, we develop a new conceptual framework that explicitly considers
20 the links between landscape fragmentation, the supply of services, and the flow
21 of services to people. We argue that fragmentation's effects on ecosystem service
22 flow can actually be positive or negative and use our framework to construct
23 testable hypotheses about the effects of fragmentation on final ecosystem service
24 provision. Empirical efforts to apply and test this framework are critical to
25 improve landscape management for multiple ecosystem services.

26

27 **Keywords:** landscape fragmentation, ecosystem services, ecosystem service
28 flow, ecosystem service supply, biodiversity

29 **Landscape fragmentation: the need to reconceptualize for ecosystem**
30 **services**

31 Humans continue to heavily modify natural ecosystems around the world,
32 with negative consequences for biodiversity (see Glossary) and natural capital
33 [1,2]. At the same time, demand for ecosystems to provide benefits, or services,
34 to society is growing rapidly [3]. This has significantly increased the need to
35 understand and manage landscapes simultaneously for ecosystem services and
36 biodiversity. Recently, the potential of managing landscape structure [4-6], and
37 in particular landscape fragmentation [7,8], for these multiple goals has been
38 highlighted. Interest in landscape fragmentation - the breaking apart of areas of
39 natural land cover into smaller pieces independent of a change in the amount of
40 natural land cover - has a long history in ecology [9]. Consequently, a well-
41 developed understanding exists of its effects on biodiversity and ecosystem
42 functioning [10]. However, the shift in research interest from biodiversity
43 towards the concept of ecosystem services has recast what before were solely
44 ecological questions into social-ecological ones [11-13]. This recasting means
45 that predictions about the ecological effects of landscape fragmentation on
46 biodiversity and ecosystem functioning are unlikely to translate directly into
47 ecosystem service provision. This will be especially true if fragmentation has
48 contrasting effects on people and how they interact with ecosystems to produce
49 ecosystem services compared to biodiversity and ecosystem functioning. It is
50 therefore critical to rethink how fragmentation alters all of the components of
51 ecosystem service provision in order to improve landscape management for
52 multiple services.

53 Ecosystem service provision depends on three elements: *supply*, *demand*,
54 and *flow* (Figure 1), each of which can respond differently to landscape
55 fragmentation. Ecosystem service supply is the potential for natural capital to
56 generate a benefit for people, irrespective of it being realized or used [14]. In
57 turn, ecosystem service demand is the level of service provision desired or
58 required by people, and is influenced by human needs, values, cultures,
59 institutions, and built capital [15]. Finally, for ecosystem service provision to be
60 realized, people must interact with ecosystems to gain a benefit. This interaction
61 connects service supply with demand to produce a service flow: the actual
62 delivery of a service to people to be used or enjoyed [15].

63 Here, we argue that the effects of fragmentation on ecosystem service
64 supply and flow can either complement or oppose each other, leading to
65 contrasting net effects on service provision. Ecosystem service supply depends
66 on the presence of particular species, ecosystems, or ecological processes that
67 are often negatively affected by fragmentation. In contrast, most ecosystem
68 service flows depend on the distribution and movement of organisms, matter,
69 and people between areas of natural and anthropogenic land cover. For example,
70 fragmentation of forests from logging, road construction, or agricultural and
71 urban expansion can alter plant species composition and growth, negatively
72 affecting water quality regulation and carbon sequestration [16,17]. At the same
73 time, this fragmentation can improve forest access, increasing timber harvesting,
74 hunting, wild food foraging, and park visits [18,19]. Thus, by altering the
75 arrangement of areas of service supply and demand, or humans and natural
76 capital across a landscape, fragmentation can modify ecosystem service supply,
77 movements critical for service flow, and ultimately service provision.

78 That landscape fragmentation simultaneously affects ecosystem service
79 supply and flow has not, thus far, been widely acknowledged in the development
80 and application of the ecosystem service concept. The majority of ecosystem
81 service studies that consider fragmentation focus only on service supply [4,20]
82 and disregard demand and flow. Similarly, most ecosystem service decision-
83 support and quantification tools focus on service supply and have limited ability
84 to determine flow [21]. While tools such as InVEST
85 (naturalcapitalproject.org/InVEST.html) and ARIES (ariesonline.org) aim to
86 better quantify service flows across landscapes, integration of this information
87 into decision-making remains limited and is still mainly focused on service
88 supply. Consequently, predictions about how landscape fragmentation will affect
89 ecosystem service provision are likely to be incorrect. This has important
90 implications for landscape planning to optimize service provision.

91 To spur research in this area, we present a conceptual framework that
92 links fragmentation explicitly with ecosystem service supply and flow, and use it
93 to make testable predictions about the effects of landscape fragmentation on
94 ecosystem service provision. We discuss how fragmentation could drive
95 tradeoffs and synergies among services, highlighting the implications for policy
96 and planning, and identify future research priorities for investigating the role of
97 landscape fragmentation on ecosystem service provision.

98

99 **Linking fragmentation to ecosystem service supply and flow**

100 Here, we identify specific mechanisms by which landscape fragmentation,
101 independent of the loss of natural land cover, affects service supply and flow
102 (Figure 1), and the ultimate consequences of these relationships for service

103 provision. A planning issue of critical importance in many human-dominated
104 landscapes is how spatially to arrange areas of natural land cover within the
105 human-dominated matrix [22,23]. While we recognize that alteration of the
106 spatial arrangement of natural land cover also has important consequences for
107 landscape heterogeneity, our framework simplifies this complexity by focusing
108 on fragmentation of natural land cover. We feel this is a necessary first step to
109 better develop a spatially explicit landscape-scale understanding of ecosystem
110 services.

111

112 *Fragmentation and ecosystem service supply*

113 Fragmentation tends to drive biodiversity loss and shifts in ecosystem
114 function [24,25], although a variety of responses can occur, especially at low or
115 intermediate levels of fragmentation [9]. Fragmentation often reduces the ability
116 of plant and animal species to move across landscapes, interrupting daily
117 movements between foraging and breeding habitat, dispersal events, and
118 migration [10]. In addition, smaller habitat patches support fewer species,
119 contain smaller populations that are at greater risk of extinction [26], and have
120 increased edge effects that can negatively affect the persistence of native species
121 [27]. Each of these different effects of fragmentation can result in degradation of
122 the natural capital and biodiversity that contribute to service supply (Figure 1).

123 There is widespread evidence that biodiversity influences or is strongly
124 correlated with the supply of many ecosystem services [28,29]. For example,
125 increased tree species richness [30] and plant diversity [6] are each associated
126 with an increased supply of multiple ecosystem services. In particular,
127 biodiversity is increasingly important as the number of services considered

128 increases [31]. Thus, if biodiversity declines with landscape fragmentation, as is
129 commonly observed [10], ecosystem service supply will also likely be lost.

130 Pollination and pest regulation are among the best-studied examples
131 where landscape fragmentation drives this relationship. Increased species and
132 functional diversity in pollinator or arthropod predator communities can
133 increase service supply [32,33]. In turn, this diversity can be enhanced by
134 increased forest and grassland connectivity or increased landscape complexity
135 (smaller fields, more hedgerows) across agricultural landscapes [34,35].
136 Fragmentation can also affect forest plant diversity and the supply of carbon
137 storage and sequestration [17,36], although this effect is not universal [37].
138 Similarly, fragmentation of marine ecosystems and rivers can have significant
139 effects on aquatic biodiversity and fish abundance important for commercial
140 fisheries [38,39]. Unfortunately, most of these examples only quantify service
141 supply and not actual flows to people, which might be affected very differently by
142 fragmentation.

143

144 *Fragmentation and ecosystem service flow*

145 For most ecosystem services, their flow depends on the movement of
146 organisms, matter, energy, and/or people across landscapes to connect spatially
147 separate locations of supply and demand (Figure 1)[20]. For example, pollination
148 depends on the movement of native pollinators from fragments of non-crop
149 vegetation into fields [40], drinking water provision relies on the flow of above-
150 and below-ground water to areas of collection or consumption [41], and the
151 movement of people to fishing locations or parks is needed for fisheries and
152 recreation [42]. Conversely, some services depend on ecosystems restricting

153 flows of organisms or matter. For example, flood regulation is provided when
154 ecosystems restrict or delay water flow [43], disease regulation when the
155 movements of disease vectors to people are limited [44], and water quality
156 regulation when ecosystems capture or transform excess nutrients, sediments or
157 pollutants [41].

158 Because ecosystem service flow relies on facilitating or restricting
159 movement, landscape fragmentation can affect the magnitude and spatial pattern
160 of these flows (Box 1)[20]. Importantly, fragmentation increases the
161 interspersion of natural and anthropogenic lands, reducing distances between
162 areas of service supply and demand, and potentially increasing service flow. At
163 the same time, fragmentation affects the number, size, shape, spatial
164 arrangement, and isolation of patches of natural land cover, which in turn can
165 positively or negatively affect the flow of soil, water, energy, and organisms
166 across landscapes [4]. Thus, fragmentation can have either negative or positive
167 effects on service flow, depending on the service in question, the process of
168 landscape fragmentation, and the resulting landscape structure (Box 1). In
169 addition, the flow of some ecosystem services will be insensitive to
170 fragmentation. For example, carbon sequestration and storage provides climate
171 regulation globally regardless of its spatial location or the location of
172 beneficiaries.

173

174 **How fragmentation affects ecosystem service flow**

175 *Increased interspersion of natural and anthropogenic lands*

176 Expansion of human land-use resulting in the fragmentation of natural
177 land cover can place areas of service supply and demand in closer proximity to

178 one another. For services that rely on the juxtaposition of ecosystems and
179 people, this can increase service flows (Figure 2A). Services provided by mobile
180 organisms often fall into this category. For example, interspersion of remnant
181 forests and grasslands with cropland can maximize both pollination and pest
182 regulation services [45]. Small reservoirs of regularly-placed natural land cover
183 that provide shelter and nesting resources can more evenly distribute pollinators
184 across agricultural landscapes and are predicted to maximize the flow of
185 pollination services [22]. Similarly, regularly-spaced forest patch and hedgerow
186 reservoirs of arthropod predators are needed to ensure an even flow of pest
187 regulation to agricultural fields [46,47].

188 Increased fragmentation can also improve people's access to ecosystems
189 to obtain recreational and health benefits. Increased visitation to parks and
190 previously inaccessible wilderness areas when roads and trails are built can
191 increase fishing, hunting, timber harvesting, and land clearing [18,19]. Similarly,
192 in urban areas having nearby green spaces increases accessibility and can
193 improve human health and well-being [48,49]. We predict that these effects of
194 fragmentation on patterns of human movement, while often overlooked in the
195 literature [4], will be as common and important for ecosystem service flow as
196 those on the movement of other organisms.

197 Increased interspersion of people, their activities, and ecosystems can
198 also increase flows of ecosystem disservices (damages or costs to people from
199 ecosystems). For example, the spread of human diseases via biotic vectors is
200 often greater when human habitation occurs in close proximity to natural areas.
201 For Lyme's disease in North America, increased interspersion of people and
202 forests is highly correlated with disease prevalence [50,51].

203

204 *Increased isolation of patches of natural land cover*

205 By isolating patches of natural land cover and reducing patch sizes,
206 fragmentation can have negative effects on the movement of organisms and
207 matter (Figure 2B). This is especially true if the intervening matrix impedes
208 movement between patches. For services provided by mobile organisms [52],
209 including pollination and seed dispersal, isolation can negatively affect service
210 flow. For example, seed dispersal can be highly sensitive to forest fragmentation
211 by agriculture, especially the loss of small forest patches that maintain landscape
212 connectivity [53]. Services that rely on the movement of water can also be
213 disproportionately affected. The presence of dams has fragmented most of
214 Earths' major river systems, reducing water flow and the movement of people
215 along these rivers, altering water provision to people, water quality regulation
216 [54], and opportunities for recreation [55,56].

217

218 *Decreased patch size and increased edge*

219 Reduced patch size can decrease visitation rates and ecosystem service
220 flows, for both organisms and people (Figure 2C). For example, smaller fields
221 often experience less pollinator visitation compared to larger fields, with
222 consequences for pollination and other services provided by mobile organisms
223 [34,57]. Similarly, small parks attract fewer visitors from surrounding urban
224 areas [58], reducing recreation [59] and other cultural services.

225 For those services that depend on restricting movement, increases in edge
226 and edge:area ratio can have a variety of effects, either reducing or increasing
227 service flow to people (Figure 2D). For example, fragmentation of areas of

228 natural land cover by agriculture can result in greater vegetation-field edge and
229 increased soil erosion [60,61] and nutrient loss [62,63], with consequences for
230 downstream water quality. Contrastingly, linear patches of vegetation such as
231 hedgerows can fragment the cropland matrix of agricultural landscapes,
232 intercepting pesticides and odors and increasing air quality regulation [64,65].
233 Other directionally-provided ecosystem services, such as storm protection and
234 flood regulation might also be improved by more linear wetlands [66].

235

236 *Consequences for ecosystem service provision*

237 The varied processes by which fragmentation affects landscape structure
238 and heterogeneity, and thereby service flow, means that fragmentation's effects
239 on supply and flow can be in parallel or opposition. We argue that this will result
240 in a variety of landscape-scale fragmentation effects on the provision of different
241 services, and hypothesize that three broad categories of effects are possible (Box
242 2). For example, when the effects of fragmentation on supply and flow oppose
243 each other, service provision will peak at intermediate levels of fragmentation
244 (Figure 3F). These three categories of relationships provide testable predictions
245 of the effects of fragmentation on service provision.

246 The diverse effects of fragmentation on service provision will also drive
247 positive and negative relationships between services in fragmented landscapes
248 as each responds differently to the modified landscape structure, even if the
249 services themselves do not interact strongly [67]. Importantly, our framework
250 predicts that tradeoffs and synergies between ecosystem services might not
251 always be unidirectional or constant, but could vary depending on the level of
252 landscape fragmentation. Thus, we predict that managing landscape structure

253 for ecosystem services does not simply involve minimizing fragmentation, but
254 requires a much more complete understanding of the effects of landscape
255 structure on service provision.

256

257 **Challenges for ecosystem service science and policy**

258 The challenge of incorporating the ecosystem services paradigm into
259 environmental policy and landscape planning is increasingly being recognized
260 [68,69]. The next major challenge is to develop a body of predictive theory to
261 support policy and planning activities, similar to that currently present in
262 biodiversity-fragmentation research. In this context, ecosystem service research
263 needs to move away from simply quantifying and mapping the biophysical
264 supply of services [70], and towards identifying locations of service demand, and
265 potential pathways and magnitudes of service flow [15,20]. Understanding these
266 different aspects of service provision and what features of landscape structure,
267 fragmentation, and heterogeneity control them will significantly improve the
268 ability to manage landscapes for ecosystem services. Our framework is a first
269 step towards a more robust theory linking landscape structure with ecosystem
270 services.

271 We propose that ecosystem service supply will decline with increasing
272 fragmentation, but that the flow of ecosystem services to beneficiaries can
273 increase or decrease. Thus, fragmentation of the landscape can either enhance or
274 degrade ecosystem service provision (Box 2). We also argue that the responses
275 of ecosystem service flow to fragmentation are driven by: (a) increased
276 interspersion of anthropogenic and natural lands, (b) increased isolation of
277 patches of natural land cover, and (c) reduced patch sizes and increased amounts

278 of edge. These predictions reflect a number of important gaps in current
279 knowledge and highlight a number of key research questions that will best
280 address them (Box 3). In particular, testing our hypotheses across landscape
281 gradients of fragmentation by quantifying the supply, demand, and flow of
282 multiple services is an essential next step. Only in this way will the mechanisms
283 by which fragmentation drives both service provision and tradeoffs between
284 services be identified. Describing the precise form of the relationships between
285 fragmentation and service provision, and identifying if distinct classes of
286 relationships exist, similar to those in our framework, are also critical questions
287 for future research.

288 Landscape planning almost always involves decisions about the spatial
289 arrangement of conflicting land-uses that influence the level of landscape
290 fragmentation (e.g. [71]). Active urban and rural landscape planning could
291 benefit substantially from a more nuanced understanding of the relationships
292 between landscape fragmentation and heterogeneity, and ecosystem service
293 provision. Yet implications for other globally relevant policy challenges are
294 equally important. Understanding when and why fragmentation inhibits or
295 enhances ecosystem service provision is central to the land sparing versus land
296 sharing (or wildlife-friendly farming) debate [23,72]. This is also true for
297 designing rules to improve the effectiveness and co-benefits from trades in
298 carbon markets (e.g. REDD+)[73], biodiversity (e.g. offsetting, agri-environment
299 schemes) [5,74], and other ecosystem services (e.g. water quality). Market-based
300 approaches to stimulate desirable land-use outcomes are also increasingly
301 incorporating effects of spatial configuration [75], but currently incorporate only
302 a simple understanding of the consequences of fragmentation. Thus,

303 understanding the effects of fragmentation on ecosystem services is of critical
304 importance for developing effective policy mechanisms.

305

306 **Concluding Remarks**

307 Our conceptual framework highlights the vital importance of
308 understanding how fragmentation of natural land cover affects service supply
309 and flow and the different ecological and social components of ecosystem service
310 provision. Incorporating these effects into ecosystem service assessments is
311 critical to develop effective tools that can help structure landscapes to provide
312 multiple ecosystem services. In many ways, the field of ecosystem services is
313 ideally placed to address this challenge; many studies already work at large
314 spatial scales across landscapes with different levels of fragmentation, and
315 incorporate data from a diversity of sources, including ecological, remote
316 sensing, and social survey data. What is needed now is increased empirical
317 research into the exact nature of the relationships between fragmentation and
318 ecosystem service supply and flow. As the ecosystem services concept is
319 increasingly incorporated into decision-making and planning activities, the need
320 to improve understanding of ecosystem service provision at the landscape-scale
321 is fundamentally important.

322

323 **Acknowledgements**

324 We thank Kerrie Wilson, Jessie Wells, Marta Pascual Altares, Rhiannon
325 Caynes, and the Environmental Decision Group's Ecosystem Services discussion
326 group for helpful comments. This work was supported by an Australian Research
327 Council Discovery Project (DP130100218); the Australian Research Council's

- 328 Centre of Excellence for Environmental Decisions; a Natural Environment
- 329 Research Council Grant (NE/J015237/1) to KJG; Chile Ministry of Education, and
- 330 CSIRO Integrative Natural Resource Management postgraduate fellowships to
- 331 MMH; and a COLCIENCIAS grant to AFSC.

332 **Figure 1.** A conceptual diagram of the effects of landscape fragmentation on the
333 provision of ecosystem services. Fragmentation alters ecosystem service supply
334 by affecting natural capital. This occurs when fragmentation affects the
335 movement and distribution of organisms, matter, and energy across a landscape,
336 with consequences for the biodiversity and ecosystem functions that are
337 important for service provision. Fragmentation also affects patterns of human
338 distribution, activities, and movement across the landscape. Combined, these
339 effects influence the magnitude and spatial pattern of ecosystem service flows
340 that connect areas of service supply to areas of demand. Thus, ecosystem service
341 flows, and ultimately service provision, depend on how landscape fragmentation
342 and the resulting landscape structure affect the movement and distribution of
343 both ecosystems and people. In turn, the benefit derived from an ecosystem
344 service affects service demand by altering human wellbeing and needs. This
345 demand then drives human activities that alter landscape fragmentation (*dashed*
346 *arrow*). Ecosystem service provision can also directly affect natural capital
347 (*dashed arrow*) through over-exploitation. Adapted from [14].

348

349 **Box 1. What is landscape fragmentation and how does it affect ecosystem**
350 **service flow?**

351 Landscape fragmentation is the breaking up of larger areas of natural land
352 cover into smaller, more isolated patches, independent of a change in the total
353 area of natural land cover (Figure 2). Landscape fragmentation causes three
354 main interconnected changes to patches of natural land cover across a
355 landscape: (i) an increase in the isolation of patches and their interspersion with
356 the surrounding human-dominated land (e.g., agricultural or urban areas), (ii) an

357 increase in the number of patches and the amount of patch edge, and (iii) a
358 decrease in average patch area [9]. Simultaneously, the surrounding human-
359 dominated portion of the landscape can become more connected as
360 fragmentation proceeds, with important consequences for the movement and
361 abundance of species that inhabit this portion of the landscape [52,76].

362 Thus, landscape fragmentation results in a number of interrelated effects
363 for landscape structure, including changes to landscape configuration and
364 heterogeneity. This means that a variety of mechanisms and effects on ecosystem
365 service flow are possible (Figure 2). Fragmentation affects ecosystem service
366 flows by facilitating or interrupting movement of organisms, matter, energy, and
367 people across landscapes. This includes the daily movements of mobile
368 organisms like pollinators and insect predators across agricultural landscapes;
369 long-distance migrations; directional overland flows of water and the nutrients,
370 pollutants, and eroded soil it contains; ocean and atmospheric currents at
371 multiple spatial scales; and the movement of people across landscapes. The final
372 effect of fragmentation on service provision will depend heavily on these
373 processes and the key species, ecosystem functions, biophysical flows, and
374 human activities that underlie each service, as well as the exact form and amount
375 of landscape fragmentation that takes place. Additionally, the scale at which
376 fragmentation takes place relative to ecosystem service flow will also change
377 how it affects service provision.

378

379 **Figure 2.** The mechanisms by which landscape fragmentation, independent of a
380 change in the area of natural land cover, can affect ecosystem service flow.

381 Locations of natural land cover and ecosystem service supply (*green areas*)

382 provide ecosystem service flows (*red* arrows) and benefits (*red* areas) to the
383 human-dominated matrix (*light brown* areas) that are affected by landscape
384 fragmentation. Ecosystem service flows of organisms and people (*arrows*) can
385 depend on proximity to natural areas (**A**) and will therefore be influenced by the
386 interspersion of natural and anthropogenic land cover across the landscape (e.g.,
387 recreation, pollination, waste treatment, pest regulation). At the same time,
388 increased isolation of patches and reduced connectivity (**B**), as well as decreased
389 patch size (**C**), can decrease service flow in fragmented landscapes (e.g.,
390 pollination, seed dispersal, cultural services, watercourse recreation, water
391 provision and regulation). Finally, for services that depend on restricting
392 movement across landscapes, increased edge amounts with fragmentation (**D**)
393 can have positive (e.g., storm protection, air quality regulation) or negative (e.g.,
394 water quality or soil erosion regulation) effects on ecosystem service flow. In
395 each panel, the area of natural land cover and ecosystem service supply is
396 unchanged between intact and fragmented landscapes. Adapted from [66].

397

398 **Box 2. Combining the effects of fragmentation on ecosystem service supply**
399 **and flow**

400 Our conceptual framework predicts that a range of relationships between
401 landscape fragmentation and final ecosystem service provision are possible
402 depending on the specific processes by which fragmentation affects service
403 supply and flow (Figure 3). While a range of effects is likely, we identify three
404 general categories of effects:

405 (1) *Double Whammy*: fragmentation negatively affects both supply and flow,
406 resulting most often in rapid and dramatic decreases in ecosystem service

407 provision with fragmentation. We predict this relationship for services
408 where reduced connectivity and decreased patch size drive reductions in
409 service flow (e.g., water provision and regulation, watercourse recreation,
410 and pollination and pest regulation at high levels of landscape
411 fragmentation).

412 (2) *Compensating*: the effects of fragmentation on flow oppose those on
413 supply, resulting in increased service provision at intermediate levels of
414 fragmentation. The exact level of fragmentation that maximizes service
415 provision depends on the strength and shape of the relationship between
416 fragmentation and service flow. Services where interspersed natural
417 land cover and human-dominated areas determines service flow should
418 respond in this way (e.g., recreation, cultural and aesthetic services,
419 genetic resources, pollination, and pest regulation)

420 (3) *Supply Driven*: ecosystem service flows are insensitive to fragmentation,
421 therefore final service provision is simply a function of the effects of
422 fragmentation on service supply. Examples include carbon sequestration,
423 carbon storage, and the existence value of biodiversity.

424 Because there is a wide range of possible patterns of ecosystem service provision
425 with fragmentation, this will drive synergies and tradeoffs between services in
426 fragmented landscapes. For example, services that respond in ‘Double Whammy’
427 or ‘Supply Driven’ ways to fragmentation might show positive relationships
428 across landscapes as fragmentation varies. Of course, variation in the strength of
429 these relationships will also occur (e.g., *blue* versus *red* lines in Figure 3E).

430 Contrastingly, tradeoffs might occur among services following a ‘Compensating’
431 relationship. Here, the strength of the trade-offs between services will depend on

432 the level of fragmentation and resulting landscape structure. Tradeoffs and
433 synergies between services and switches between the two could also occur
434 within the 'Compensating' category as levels of fragmentation vary (e.g., *green*
435 *dashed* versus *blue solid* line in Figure 3F). Thus, our framework predicts that
436 tradeoffs and synergies between services might not always be unidirectional or
437 constant, but will vary depending on the level of landscape fragmentation.

438

439 **Figure 3.** Effects of landscape fragmentation on the supply and the flow of
440 ecosystem services will affect the final relationship between landscape
441 fragmentation and ecosystem service provision. Landscape fragmentation, by
442 reducing biodiversity and ecosystem function, is **(A)** predicted to reduce
443 ecosystem service supply (three alternative possible trajectories are shown: *red*,
444 *green*, and *blue* lines). At the same time, the amount of flow per unit of ecosystem
445 service supply to beneficiaries can also be affected **(B)** negatively, **(C)** positively,
446 or **(D)** be insensitive to landscape fragmentation (e.g., carbon sequestration),
447 with a range of relationships possible (e.g., *solid*, *dashed*, and *dotted lines*).
448 Combining ecosystem service supply and flow multiplicatively **(E,F,G)** will result
449 in distinct relationships between landscape fragmentation and ecosystem
450 service provision. Each of the trend lines in **(E,F,G)** is a combination of the lines
451 in the plots above. Note that some lines overlap in **(E)** and for clarity not all
452 possible combinations of supply and flow are shown; the *grey* lines in **(E)** show
453 what provision would be if flow was insensitive to fragmentation.

454

455 **Box 3. Outstanding questions about the effects of fragmentation on**
456 **ecosystem services**

457 (1) What are the specific relationships between landscape fragmentation and
458 ecosystem service supply and flow for different services? While there is
459 likely wide variation in the form of these relationships, this has yet to be
460 quantified. This is a key first step to creating landscape management tools
461 for ecosystem services that deal with fragmentation.

462 (2) What are the important mechanisms by which fragmentation affects
463 service flow for different ecosystem services, and do these vary
464 depending on spatial scale considered? We identify four potential
465 mechanisms, but their relative importance across different services is
466 largely unknown. Understanding these mechanisms is key to creating a
467 predictive framework for the effects of landscape fragmentation on
468 ecosystem service provision.

469 (3) Can the relationships between fragmentation and ecosystem service flow
470 and final provision be generalized for specific categories of services?
471 While we identify three broad potential categories (Figure 3), there might
472 be additional categories or there might be instances where relationships
473 between services and fragmentation are idiosyncratic depending on the
474 scale of fragmentation or other biophysical and social factors. While we
475 hypothesize that this is unlikely, it has yet to be tested.

476 (4) How are positive or negative relationships between ecosystem services
477 affected by landscape fragmentation? Our framework predicts that these
478 relationships might not be constant, but could vary across gradients of
479 fragmentation or landscape structure. The prevalence and actual form of
480 these relationships need to be tested in real landscapes.

481 (5) How can the effects of fragmentation on ecosystem service provision be
482 effectively integrated into decision-making? The causes of fragmentation
483 across landscapes are varied and it can often be driven by external factors
484 such as demand for ecosystem services from distant locations. Therefore,
485 effectively integrating knowledge about the effects of fragmentation into
486 landscape planning will likely be difficult and effective paths to do this are
487 yet to be explored.

488 (6) What is the most important component of ecosystem service provision
489 (i.e., supply or flow) to understand with respect to landscape planning?
490 With limited resources available to investigate how fragmentation affects
491 both service supply and flow, determining which is most important for
492 landscape management is critical to efficient decision-making.

493 **Glossary**

494

495 **Benefit:** the ways in which ecosystems improve human wellbeing via the
496 provision of ecosystem services. Constituents of human wellbeing include
497 materials essential for life, and contributions to health, security, social relations,
498 and freedom of choice and action [77].

499 **Biodiversity:** the variability among living organisms from all sources including,
500 *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological
501 complexes of which they are part; this includes diversity within species, between
502 species and of ecosystems. Defined here following the 1993 Convention on
503 Biological Diversity (CBD) meaning of 'biological diversity', which we assume is
504 equivalent to 'biodiversity' (www.cbd.int/convention/articles).

505 **Connectivity:** the degree to which a landscape facilitates the movement of
506 organisms and matter [78]. We use the term to include both biotic connectivity
507 (movement of organisms) and abiotic connectivity (movement of water,
508 nutrients, and soil) across landscapes.

509 **Ecosystem function:** the flow of energy and materials through the arrangement
510 of biotic and abiotic components of an ecosystem that allow or could allow
511 natural systems to provide ecosystem services [79].

512 **Ecosystem service:** defined broadly, the biophysical and social conditions and
513 processes by which people, directly or indirectly, obtain benefits from
514 ecosystems that sustain and fulfill human life [77].

515 **Ecosystem service demand:** the level of service provision desired or required
516 by people. Demand is influenced by human needs, values, institutions, built
517 capital, and technology [15].

518 **Ecosystem service flow:** the actual delivery to or realization of an ecosystem
519 service by people. Ecosystem service flow depends on both the supply of and
520 demand for a service [14,15] as well as the movement of organisms, matter, and
521 people [4].

522 **Ecosystem service supply:** the full potential of ecological functions or
523 biophysical elements in an ecosystem to provide a given ecosystem service,
524 without consideration of whether humans recognize, use, or value that function
525 or element [14,15].

526 **Landscape:** a heterogeneous area composed of interacting ecosystems that is
527 repeated in similar form throughout, including both natural and anthropogenic
528 land covers, across which humans interact with their environment [80].

529 **Landscape fragmentation:** the breaking apart of areas of natural land cover
530 into several smaller areas within a human-dominated matrix, without any
531 change in the area of natural land cover [9].

532 **Landscape heterogeneity:** the amount of variation in landscape structure
533 (composition and configuration) at a particular spatial scale across a landscape.
534 Landscape heterogeneity is affected by landscape fragmentation through
535 changes to patterns of spatial complexity.

536 **Landscape structure:** the arrangement of land covers and land uses across a
537 landscape. Broadly, it includes landscape composition (how much of each land
538 cover or land use that exists), configuration (the spatial pattern of these land
539 cover or land use types), and connectivity.

540 **Landscape matrix:** the surrounding portion of the landscape in which
541 fragments of natural land cover are located. In most cases we consider the matrix
542 to be the human-dominated or disturbed areas of the landscape (e.g., agricultural

543 fields, urban areas, cleared land). Characteristics of the matrix can be important
544 for determining landscape connectivity and ecosystem service flow.
545 **Natural capital:** the stock of natural ecosystems, including all of their biological
546 and physical features that supply flows of ecosystem services to people.

547 **References**

- 548 1 Butchart, S.H.M. *et al.* (2010) Global biodiversity: indicators of recent
549 declines. *Science* 328, 1164–1168
- 550 2 Foley, J.A. *et al.* (2011) Solutions for a cultivated planet. *Nature* 478, 337–
551 342
- 552 3 Carpenter, S.R. *et al.* (2009) Science for managing ecosystem services:
553 Beyond the Millennium Ecosystem Assessment. *Proc. Natl. Acad. Sci. U.S.A.*
554 106, 1305–1312
- 555 4 Mitchell, M.G. *et al.* (2013) Linking landscape connectivity and ecosystem
556 service provision: current knowledge and research gaps. *Ecosystems* 16,
557 894–908
- 558 5 Ekroos, J. *et al.* (2014) Optimizing agri-environment schemes for
559 biodiversity, ecosystem services or both? *Biol. Conserv.* 172, 65–71
- 560 6 Werling, B.P. *et al.* (2014) Perennial grasslands enhance biodiversity and
561 multiple ecosystem services in bioenergy landscapes. *Proc. Natl. Acad. Sci.*
562 *U.S.A.* 111, 1652–1657
- 563 7 Ziter, C. *et al.* (2013) Functional diversity and management mediate
564 aboveground carbon stocks in small forest fragments. *Ecosphere* 4, art85
- 565 8 Dobbs, C. *et al.* (2014) Multiple ecosystem services and disservices of the
566 urban forest establishing their connections with landscape structure and
567 sociodemographics. *Ecol. Indic.* 43, 44–55
- 568 9 Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annu. Rev.*
569 *Ecol. Evol. S.* 34, 487–515
- 570 10 Fischer, J. and Lindenmayer, D.B. (2007) Landscape modification and habitat
571 fragmentation: a synthesis. *Global. Ecol. Biogeogr.* 16, 265–280

- 572 11 Hughes, T.P. *et al.* (2005) New paradigms for supporting the resilience of
573 marine ecosystems. *Trends Ecol. Evol.* 20, 380–386
- 574 12 Chapin, F.S. *et al.* (2010) Ecosystem stewardship: sustainability strategies
575 for a rapidly changing planet. *Trends Ecol. Evol.* 25, 241–249
- 576 13 Mace, G.M. (2014) Whose conservation? *Science* 345, 1558–1560
- 577 14 Tallis, H. *et al.* (2012) A global system for monitoring ecosystem service
578 change. *BioScience* 62, 977–986
- 579 15 Villamagna, A.M. *et al.* (2013) Capacity, pressure, demand, and flow: A
580 conceptual framework for analyzing ecosystem service provision and
581 delivery. *Ecol. Complex* 15, 114–121
- 582 16 Edwards, D.P. *et al.* (2014) Maintaining ecosystem function and services in
583 logged tropical forests. *Trends Ecol. Evol.* 29, 511–520
- 584 17 Pütz, S. *et al.* (2014) Long-term carbon loss in fragmented Neotropical
585 forests. *Nature Commun.* 5, 5037
- 586 18 Peres, C.A. and Lake, I.R. (2003) Extent of nontimber resource extraction in
587 tropical forests: accessibility to game vertebrates by hunters in the Amazon
588 basin. *Conserv. Biol.* 17, 521–535
- 589 19 Trombulak, S.C. and Frissell, C.A. (2000) Review of ecological effects of roads
590 on terrestrial and aquatic communities. *Conserv. Biol.* 14, 18–30
- 591 20 Bagstad, K.J. *et al.* (2013) Spatial dynamics of ecosystem service flows: a
592 comprehensive approach to quantifying actual services. *Ecosystem Services*
593 4, 117–125
- 594 21 Bagstad, K.J. *et al.* (2013) A comparative assessment of decision-support
595 tools for ecosystem services quantification and valuation. *Ecosystem Services*
596 5, 27–39

- 597 22 Brosi, B.J. *et al.* (2008) Optimal design of agricultural landscapes for
598 pollination services. *Conserv. Lett.* 1, 27–36
- 599 23 Lin, B.B. and Fuller, R.A. (2013) Sharing or sparing? How should we grow
600 the world's cities? *J. Appl. Ecol.* 50, 1161–1168
- 601 24 Leibold, M.A. *et al.* (2004) The metacommunity concept: a framework for
602 multi-scale community ecology. *Ecol. Lett.* 7, 601–613
- 603 25 Gonzalez, A. *et al.* (2009) Biodiversity as spatial insurance: the effects of
604 habitat fragmentation and dispersal on ecosystem functioning. In
605 *Biodiversity, Ecosystem Functioning, and Human Wellbeing* (Naeem, S. *et al.*,
606 eds), pp. 134–146, Oxford University Press
- 607 26 Dobson, A. *et al.* (2006) Habitat loss, trophic collapse, and the decline of
608 ecosystem services. *Ecology* 87, 1915–1924
- 609 27 Harper, K.A. *et al.* (2005) Edge influence on forest structure and
610 composition in fragmented landscapes. *Conserv. Biol.* 19, 768–782
- 611 28 Cardinale, B.J. *et al.* (2012) Biodiversity loss and its impact on humanity.
612 *Nature* 486, 59–67
- 613 29 Balvanera, P. *et al.* (2006) Quantifying the evidence for biodiversity effects
614 on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156
- 615 30 Gamfeldt, L. *et al.* (2013) Higher levels of multiple ecosystem services are
616 found in forests with more tree species. *Nature Commun.* 4, 1340
- 617 31 Isbell, F. *et al.* (2011) High plant diversity is needed to maintain ecosystem
618 services. *Nature* 477, 199–202
- 619 32 Hoehn, P. *et al.* (2008) Functional group diversity of bee pollinators
620 increases crop yield. *P. Roy. Soc. B-Biol. Sci.* 275, 2283–2291
- 621 33 Letourneau, D.K. *et al.* (2009) Effects of natural enemy biodiversity on the

622 suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev.*
623 *Ecol. Evol. S.* 40, 573–592

624 34 Klein, A.-M. *et al.* (2012) Wild pollination services to California almond rely
625 on semi-natural habitat. *J. Appl. Ecol.* 49, 723–732

626 35 Chaplin-Kramer, R. *et al.* (2011) A meta-analysis of crop pest and natural
627 enemy response to landscape complexity. *Ecol. Lett.* 14, 922–932

628 36 Numata, I. *et al.* (2011) Carbon emissions from deforestation and forest
629 fragmentation in the Brazilian Amazon. *Environ. Res. Lett.* 6, 044003

630 37 Ziter, C. *et al.* (2014) Temperate forest fragments maintain aboveground
631 carbon stocks out to the forest edge despite changes in community
632 composition. *Oecologia* 176, 893–902

633 38 Ziv, G. *et al.* (2012) Trading-off fish biodiversity, food security, and
634 hydropower in the Mekong River Basin. *Proc. Natl. Acad. Sci. U.S.A.* 109,
635 5609–5614

636 39 Edwards, H. *et al.* (2010) Incorporating ontogenetic dispersal, ecological
637 processes and conservation zoning into reserve design. *Biol. Conserv.* 143,
638 457–470

639 40 Ricketts, T.H. *et al.* (2008) Landscape effects on crop pollination services:
640 are there general patterns? *Ecol. Lett.* 11, 499–515

641 41 Brauman, K.A. *et al.* (2007) The nature and value of ecosystem services: an
642 overview highlighting hydrologic services. *Annu. Rev. Env. Resour.* 32, 67–98

643 42 Bagstad, K.J. *et al.* (2014) From theoretical to actual ecosystem services:
644 mapping beneficiaries and spatial flows in ecosystem service assessments.
645 *Ecol. Soc.* 19, art64

646 43 Luck, G.W. *et al.* (2009) Protecting ecosystem services and biodiversity in

647 the world's watersheds. *Conserv. Lett.* 2, 179–188

648 44 Plantegenest, M. *et al.* (2007) Landscape epidemiology of plant diseases. *J.*
649 *Roy. Soc. Interface* 4, 963–972

650 45 Tschardtke, T. *et al.* (2005) Landscape perspectives on agricultural
651 intensification and biodiversity - ecosystem service management. *Ecol. Lett.*
652 8, 857–874

653 46 Bianchi, F.J.J.A. *et al.* (2010) Spatial variability in ecosystem services: simple
654 rules for predator-mediated pest suppression. *Ecol. Appl.* 20, 2322–2333

655 47 Otieno, M. *et al.* (2011) Local management and landscape drivers of
656 pollination and biological control services in a Kenyan agro-ecosystem. *Biol.*
657 *Conserv.* 144, 2424–2431

658 48 Takano, T. *et al.* (2002) Urban residential environments and senior citizens'
659 longevity in megacity areas: the importance of walkable green spaces. *J.*
660 *Epidemiol. Commun. H.* 56, 913–918

661 49 Wolch, J. *et al.* (2011) Childhood obesity and proximity to urban parks and
662 recreational resources: a longitudinal cohort study. *Health Place* 17, 207–
663 214

664 50 Jackson, L.E. *et al.* (2006) Towards landscape design guidelines for reducing
665 Lyme disease risk. *Int. J. Epidemiol.* 35, 315–322

666 51 Li, S. *et al.* (2012) Consequences of landscape fragmentation on Lyme
667 disease risk: a cellular automata approach. *Plos One* 7, e39612

668 52 Kremen, C. *et al.* (2007) Pollination and other ecosystem services produced
669 by mobile organisms: a conceptual framework for the effects of land-use
670 change. *Ecol. Lett.* 10, 299–314

671 53 Bodin, O. *et al.* (2006) The value of small size: loss of forest patches and

672 ecological thresholds in southern Madagascar. *Ecol. Appl.* 16, 440–451

673 54 Nilsson, C. *et al.* (2005) Fragmentation and flow regulation of the world's
674 large river systems. *Science* 308, 405–408

675 55 Loomis, J. (2002) Quantifying recreation use values from removing dams
676 and restoring free-flowing rivers: A contingent behavior travel cost demand
677 model for the Lower Snake River. *Water Resour. Res.* 38, 2–1 – 2–8

678 56 Whittaker, D. and Shelby, B. (2002) Evaluating instream flows for
679 recreation: Applying the structural norm approach to biophysical
680 conditions. *Leisure Sci.* 24, 363–374

681 57 Isaacs, R. and Kirk, A.K. (2010) Pollination services provided to small and
682 large highbush blueberry fields by wild and managed bees. *J. Appl. Ecol.* 47,
683 841–849

684 58 Cohen, D.A. *et al.* (2010) Parks and physical activity: why are some parks
685 used more than others? *Prev. Med.* 50, S9–12

686 59 Van Dyck, D. *et al.* (2013) Associations of neighborhood characteristics with
687 active park use: an observational study in two cities in the USA and Belgium.
688 *Int. J. Health Geogr.* 12, 26–34

689 60 Ouyang, W. *et al.* (2010) Soil erosion dynamics response to landscape
690 pattern. *Sci. Total Environ.* 408, 1358–1366

691 61 Ziegler, A.D. *et al.* (2007) Hydrological consequences of landscape
692 fragmentation in mountainous northern Vietnam: buffering of Hortonian
693 overland flow. *J. Hydrol.* 337, 52–67

694 62 Gergel, S.E. (2005) Spatial and non-spatial factors: When do they affect
695 landscape indicators of watershed loading? *Landscape Ecol.* 20, 177–189

696 63 Gémesi, Z. *et al.* (2011) Effects of watershed configuration and composition

697 on downstream lake water quality. *J. Environ. Qual.* 40, 517–527

698 64 Lazzaro, L. *et al.* (2008) Role of hedgerows in intercepting spray drift:
699 Evaluation and modelling of the effects. *Agr. Ecosyst. Environ.* 123, 317–327

700 65 Tyndall, J. and Colletti, J. (2007) Mitigating swine odor with strategically
701 designed shelterbelt systems: a review. *Agroforest. Syst.* 69, 45–65

702 66 Fisher, B. *et al.* (2009) Defining and classifying ecosystem services for
703 decision making. *Ecol. Econ.* 68, 643–653

704 67 Bennett, E.M. *et al.* (2009) Understanding relationships among multiple
705 ecosystem services. *Ecol. Lett.* 12, 1394–1404

706 68 Bateman, I.J. *et al.* (2013) Bringing ecosystem services into economic
707 decision-making: land use in the United Kingdom. *Science* 341, 45–50

708 69 Perrings, C. *et al.* (2011) The biodiversity and ecosystem services science-
709 policy interface. *Science* 331, 1139–1140

710 70 Seppelt, R. *et al.* (2011) A quantitative review of ecosystem service studies:
711 approaches, shortcomings and the road ahead. *J. Appl. Ecol.* 48, 630–636

712 71 Phalan, B. *et al.* (2011) Reconciling food production and biodiversity
713 conservation: land sharing and land sparing compared. *Science* 333, 1289–
714 1291

715 72 Fischer, J. *et al.* (2014) Land sparing versus land sharing: moving forward.
716 *Conserv. Lett.* 7, 149–157

717 73 Jantz, P. *et al.* (2014) Carbon stock corridors to mitigate climate change and
718 promote biodiversity in the tropics. *Nat. Clim. Change* 4, 138–142

719 74 Wendland, K.J. *et al.* (2010) Targeting and implementing payments for
720 ecosystem services: Opportunities for bundling biodiversity conservation
721 with carbon and water services in Madagascar. *Ecol. Econ.* 69, 2093–2107

- 722 75 Polasky, S. *et al.* (2014) Implementing the optimal provision of ecosystem
723 services. *Proc. Natl. Acad. Sci. U.S.A.* 111, 6248–6253
- 724 76 Watling, J.I. *et al.* (2011) Meta-analysis reveals the importance of matrix
725 composition for animals in fragmented habitat. *Global Ecol. Biogeogr.* 20,
726 209–217
- 727 77 Millennium Assessment (2005) *Ecosystems and human well-being: synthesis*,
728 Island Press Washington, DC.
- 729 78 Taylor, P.D. *et al.* (1993) Connectivity is a vital element of landscape
730 structure. *Oikos* 68, 571–573
- 731 79 Diaz, S. and Cabido, M. (2001) Vive la difference: plant functional diversity
732 matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655
- 733 80 Forman, R.T. and Godron, M. (1981) Patches and structural components for
734 a landscape ecology. *BioScience* 31, 733–740

Figure 1

Socioecological system

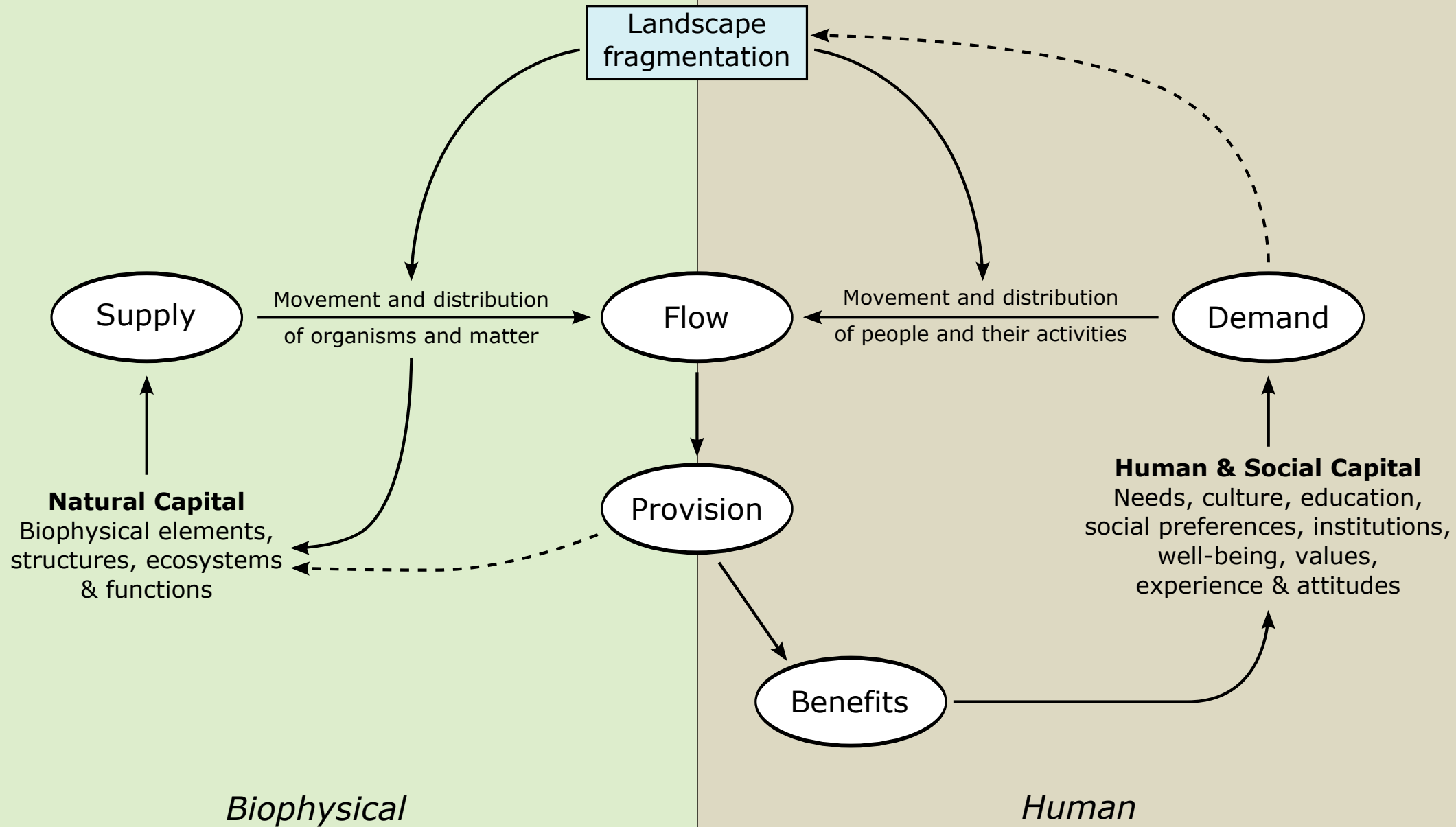
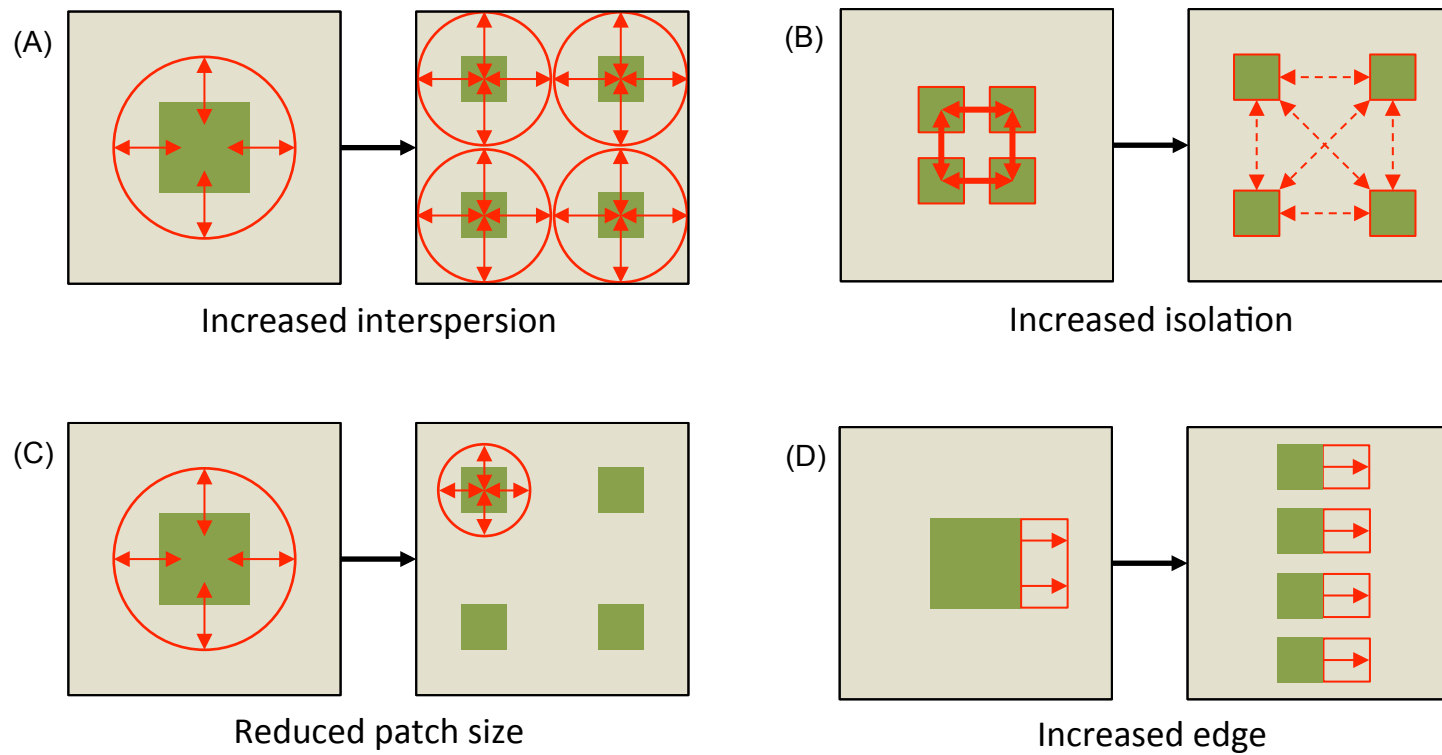


Figure 2







-  Natural land cover (location of ecosystem service supply)
-  Human-dominated land cover
-  Location of ecosystem service provision
-  Ecosystem service flow

Figure 3

