

1 **Consistent trade-offs in ecosystem services between land** 2 **covers with different production intensities**

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13 **ABSTRACT**

14 Sustaining multiple ecosystem services across a landscape requires an understanding of
15 how consistently services are shaped by different categories of land uses. Yet, this
16 understanding is generally constrained by the availability of fine-resolution data for
17 multiple services across large areas and the spatial variability of land-use effects on
18 services. We systematically surveyed published literature for New Zealand (1970 – 2015)
19 to quantify the supply of 17 services across 25 land covers (as a proxy for land use). We
20 found a consistent trade-off in the services supplied by anthropogenic land covers with a
21 high production intensity (e.g., cropping) versus those with extensive or no production. In
22 contrast, forest cover was not associated with any distinct patterns of service supply. By
23 drawing on existing research findings we reveal complementarity and redundancy
24 (potentially influencing resilience) in service supply from different land covers. This can
25 guide practitioners in shaping land systems that sustainably support human well-being.

26 *Key words:* Land-use planning, environmental management, ecosystem service bundles,
27 quantitative review, network meta-analysis.

28 CONTENTS

29	I. INTRODUCTION.....	2
30	II. METHODS.....	5
31	(1) Data collection, aggregation and calculation of effect sizes.....	6
32	(2) Data analysis	9
33	III. RESULTS.....	12
34	(1) Data coverage.....	12
35	(2) Land cover effects on individual ES	13
36	(3) Land cover effects across multiple ES	15
37	(a) Differences among ES from the land covers that supply them	15
38	(b) Differences among land covers in their supply of services.....	16
39	IV. DISCUSSION.....	17
40	V. CONCLUSIONS.....	23
41	VI. ACKNOWLEDGEMENTS	24
42	VII. AUTHOR CONTRIBUTIONS.....	24
43	VIII. REFERENCES.....	24
44	IX. SUPPORTING INFORMATION.....	33

45 I. INTRODUCTION

46 Human transformation of the Earth’s surface through land-use activities has reached an
47 unprecedented magnitude, and constitutes a major driver of global environmental change
48 (Turner, Lambin, & Reenberg, 2008; Steffen *et al.*, 2015). Humans rely on resources
49 appropriated through land use, however most of these practices affect the Earth’s
50 ecosystems in ways that undermine human well-being (Foley *et al.*, 2005). Continued

51 population growth and increased per capita consumption of resources (Godfray *et al.*,
52 2010) make it critical to find the ways to reconcile production and sustainability in land
53 systems.

54 Ecosystem services (ES) offer a framework for addressing these complex issues by
55 explicitly accounting for the benefits that ecosystems bring to society. Central to this
56 framework is the idea that human well-being is underpinned by a diverse constellation of
57 ES (MEA, 2005). Most of these ES are not accounted for in conventional land use planning
58 and management decisions which, instead, tend to focus on the production of a single ES
59 (e.g., provision of food or timber) (Robertson & Swinton, 2005; Rodríguez *et al.*, 2006). By
60 highlighting the importance of multiple over individual services, the ES framework
61 encourages decision makers to prioritize long-term well-being over immediate economic
62 reward (Guerry *et al.*, 2015; Costanza *et al.*, 2014).

63 Developing strategies that optimize ES across different land uses, or enhance multiple ES
64 within a single type of land use (Lambin & Meyfroidt, 2011), relies on understanding the
65 occurrence and interactions between different ES and their responses to management
66 interventions. To this end, important efforts have been made to map and quantify ES
67 supply (see Crossman *et al.*, 2013; Groot *et al.*, 2012; and Martínez-Harms & Balvanera,
68 2012 for reviews) and, more specifically, assess how different ES are enhanced
69 synergistically or traded-off against each other (Nelson *et al.*, 2009; Bateman *et al.*, 2013).
70 More recently, research on ES trade-offs and synergies has come together under the
71 concept of ES bundles: groups of ES that repeatedly appear together in space and/or time
72 (Raudsepp-Hearne, Peterson, & Bennett, 2010; Saidi & Spray, 2018). ES bundles can be
73 examined in terms of the supply (Queiroz *et al.*, 2015) and the demand (Ament *et al.*, 2017)
74 of ES. In either case, ES bundles can be used subsequently to identify any common
75 processes or external factors driving different ES (Mouchet *et al.*, 2014).

76 A systematic review of 51 studies on ES bundles revealed multiple approaches to bundling
77 ES and the consequent difficulties in obtaining cross-site comparisons and generalizations
78 of bundles and their drivers (Saidi & Spray, 2018). Moreover, even when the same
79 methods, datasets and groups of ES were used to identify ES bundles and their relation to

80 social-ecological variables in two regions, the results were highly inconsistent between
81 regions (Spake *et al.*, 2017) and, therefore, not generalizable to other locations. This
82 inconsistency may result from the choice of ES indicators, socio-ecological variables and
83 spatial units of analysis (Spake *et al.*, 2017). Often, studies that examine ES bundles use
84 administrative units (e.g., municipalities) as the scale at which ES are quantified (Saidi &
85 Spray, 2018). However, administrative units can mask ES associations because they: 1) are
86 variable in size (within the same hierarchical level), 2) occur at scales that are too coarse to
87 capture the fine-scale processes linked to some ES, 3) encompass heterogeneous sets of
88 land covers / land uses and 4) have boundaries that may cut across ecologically relevant
89 units (Spake *et al.*, 2017). Therefore, identifying consistent rules regarding ES bundles and
90 their drivers requires tailored analyses that focus on finer scales, such as ES measured in
91 individual plots within land cover types (Spake *et al.*, 2017).

92 Here we directly test whether there are any general rules for the effect of land use on ES
93 bundles by assessing the supply of multiple ES across land covers (as a proxy for land use)
94 at a national scale. We systematically surveyed the published literature for New Zealand
95 (1970 - 2015) to collate studies with quantitative evidence of how different land covers
96 compare against each other in processes relating to the supply of one or more ES. For each
97 study, we calculated standardized pairwise comparisons (expressed as log response ratios)
98 of land covers in their supply of individual services. We used these ratios to conduct
99 network meta-analysis for individual services and obtained, for each service, quantitative
100 estimates of service supply from individual land covers.

101 With this comprehensive evidence base, we first discuss land cover effects on individual ES
102 and then examine associations between ES to delineate any potential synergies and trade-
103 offs arising from services that are best supplied by similar or different land covers.

104 Similarly, we also examine associations between land covers based on the different ES they
105 supply. We use this to detect: 1) any land covers that may be operating as “generalists”
106 (i.e. supplying many ES) or “specialists” (i.e. supplying just a few ES) and 2) groups of land
107 covers that supply similar profiles of ES (i.e. ES bundles sensu Raudsepp-Hearne *et al.*,
108 2010). The latter includes services that are typically traded off against each other.

109 Subsequently, we test whether there are generalities regarding how categories of land
110 cover influence ES bundles (i.e. sets of ES supplied consistently across more than one land
111 cover) by testing for systematic differences between forested and non-forested habitats
112 and between exotic-species-dominated production and native non-production land covers
113 (note that we use the term production to refer to economic activity rather than primary
114 production). If they exist, these differences would suggest that production/no production,
115 forest/non-forest cover and native/exotic vegetation are attributes that drive changes in ES
116 supply across multiple land covers. Previous research has shown that attributes of single
117 land cover types can drive the value of multiple ES (Sutherland, Gergel, & Bennett, 2016)
118 and trade-offs and synergies between ES (Felipe-Lucia *et al.*, 2018). Duarte and colleagues
119 (2018) also present evidence that landscape composition metrics (e.g., percentage of
120 natural areas and of non-crop areas) affect some ES (water quality, pest regulation,
121 pollination and disease mitigation); however, their analysis did not identify specific
122 attributes of natural or non-crop areas that could shape ES supply. Our analysis extends
123 these perspectives to include attributes shared by multiple land covers, which can
124 potentially inform management decisions at broader scales and allow generalities across
125 land covers. We conclude with an example of how our findings can be used to examine the
126 effects of land cover trajectories or contrasting management decisions on landscape-scale
127 ES trade-offs.

128 **II. METHODS**

129 Unlike existing reviews and meta-analyses on ES (e.g., Howe *et al.*, 2014; Malinga *et al.*,
130 2015; Lee & Lautenbach, 2016; Nieto-Romero *et al.*, 2014), our work does not collate
131 existing ES assessments. Rather, we synthesize primary biophysical research that
132 compares land covers in relation to a large variety of measures (which we term ‘ES
133 indicators’) that indicate the supply of an ES, regardless of whether ES terminology was
134 used. Despite the growing literature on ES (Chaudhary *et al.*, 2015), our understanding of
135 ES bundles, trade-offs and synergies has traditionally been impaired by the lack of, and
136 costliness of obtaining, detailed spatial data on multiple ES from multiple land uses across
137 landscapes (Andrew *et al.*, 2015). This has led to the widespread approach of using expert

138 or model estimates of ES per land use or land cover class as input for ES assessments (see
139 Jacobs *et al.*, 2015 for a review; Aldana Domínguez *et al.*, 2019; and Chen, Chi, & Li, 2019
140 provide recent examples). Here, we propose an alternative approach that makes it possible
141 to use primary data to study land cover and ES relations by capitalizing upon existing
142 research across multiple disciplines. We use New Zealand as a case study because the high
143 levels of endemic flora and fauna and relatively recent introduction of large-scale intensive
144 agriculture make conservation-production tensions particularly acute, and necessitate
145 conservation strategies that go beyond protected areas (Craig *et al.*, 2000).

146 Our systematic review was structured according to the “Guidelines for Systematic Review
147 in Environmental Management” developed by the Collaboration for Environmental
148 Evidence (CEE, 2013). We searched the literature for quantitative comparisons of two or
149 more land covers in the supply of one or more ES within New Zealand. Our ES definitions
150 were adapted from the Millennium Ecosystem Assessment (MEA, 2005), with a total of 35
151 ES spanning across the provisioning, regulating, cultural and supporting categories
152 (Supplementary Dataset 1). Despite the debates on whether the Millennium Ecosystem
153 Assessment classification of ES leads to double counting of some services (Wallace, 2007;
154 Fisher, Turner, & Morling, 2009), we have adopted it in this study because of its wide use
155 and because our main interest was not to render a final valuation of ES (where double
156 counting would be an issue), but instead to provide a comprehensive overview of the
157 complete spectrum of direct and indirect benefits from ecosystems. Land uses, formally
158 defined as the purposes to which humans put land into use (Dale *et al.*, 2000), were
159 captured in our research as land covers (Supplementary Dataset 2), since these include
160 units that are not directly used by humans and, consequently, correspond more closely
161 with the actual experimental or sampling units of many of the documents in our search.

162 **(1) Data collection, aggregation and calculation of effect sizes**

163 Full details of the search and screening process are described in Supplementary Methods 1;
164 here we present a brief outline. We searched the Scopus database for titles, abstracts and
165 keywords with at least one match in each of the 3 components that structured our search:
166 1) “New Zealand”, 2) land cover and land use terms and 3) ES terms (see Supplementary

167 Methods 2 for the full search phrase). Land cover terms included all possible variations of
168 “land use” and “land cover” as well as the names of specific land use and land cover types
169 (both generic and specific to New Zealand). The ES component drew upon the names of
170 each service (and possible variations of these) but also included vocabulary describing
171 processes and conditions that could reflect their supply at the site scale akin to individual
172 land cover units. The search was finalized in December 2014, and was constrained to
173 include documents published from 1970 onward, to be comparable with current land use
174 regimes in New Zealand (MacLeod & Moller, 2006).

175 Our keyword search yielded 9,741 references. An initial automated screening process
176 reduced these to 4,373 publications by removing references that only mentioned a single
177 type of land cover or land use in their title, abstract and keywords. We excluded these
178 studies because measures of ES supply from single land covers could not be standardized
179 in a way that would make them comparable across studies *and* compatible with the
180 standardized land cover comparisons of ES supply that informed the rest of our meta-
181 analysis.

182 Publications with 2 or more land cover terms were scanned using Abstrackr, an interactive
183 machine learning system for semi-automated abstract screening, often used in medical
184 meta-analyses (Wallace *et al.*, 2012). By learning from the abstracts or words that a user
185 identifies as relevant during the screening process, Abstrackr can predict the likely
186 relevance of unscreened abstracts and effectively assist in the exclusion of irrelevant ones
187 (more details in Supplementary Methods 1).

188 Abstract screening yielded 914 relevant papers, which were passed on to a team of four
189 reviewers for full-text assessment and data extraction. Studies that did not have replicated
190 observations (as defined in Supplementary Methods 1) for any land covers were discarded,
191 whereas studies that contained replication on some, but not all, of the land covers were
192 kept and only data on the replicated land covers were extracted. Although we only included
193 terrestrial land covers, ES supplied by land but linked to a water body were included in our
194 analysis. Full details of how the full-text selection criteria were applied can be found in

195 Supplementary Methods 3. In total, we extracted data from 133 studies that met all
196 inclusion criteria (see Supplementary Dataset 4 for bibliographic details of each study).
197 Information on the land covers, quantitative measures of ES supply, experimental design
198 and bibliographic details for each study was collated in a database. To allow for
199 comparability across studies, individual land covers described in each study were matched
200 to the nearest category in New Zealand's Land Cover Database - LCDB (Thompson, Grüner,
201 & Gapare, 2003). This classification system includes forest, shrubland and grassland areas
202 of either predominantly native or exotic vegetation, as well as cropland and more artificial
203 surfaces such as built-up surfaces and mining areas (Supplementary Dataset 2).

204 Often, the same quantitative measure of ES supply obtained from a study (indicators,
205 presented in Supplementary Dataset 3) would be relevant to more than one ES. This
206 reflects the overlaps that exist between different ES (e.g., soil structure plays a role in both
207 soil formation and regulation of water timing and flows), and the multiple values that
208 humans can receive from a given ecosystem process. We therefore decided to assign each
209 indicator to as many ES as it was relevant to, and use this allocation in our main analysis.
210 However, to understand the influence on our results of sharing indicators between ES, we
211 also conducted the same analysis with each indicator assigned to only one ES. In
212 Supplementary Results 5 we present the results of this analysis.

213 For each indicator - ES combination we defined the general direction of the relationship by
214 determining whether larger values of the indicator would generally reflect an increase or
215 decrease in ES supply. This was done because the majority of the studies in our meta-
216 analysis did not explicitly use 'ecosystem services' terminology. Instead, they measured
217 environmental or ecological variables that could be used as indicators of ES supply,
218 provided a conceptual link could be defined between the indicator (e.g., annual water
219 discharge of a catchment) and the corresponding ES (provision of freshwater). When we
220 could not readily assign indicators to ES or determine the direction of the indicator - ES
221 relationship we consulted with experts with specialized knowledge of the field related to
222 each indicator (see Acknowledgements). Although we recognize that the relationship
223 between an indicator and a ES may be non-linear (e.g., pollination services may saturate

224 with large numbers of pollinators), in most cases it was not possible to establish a clearly
225 defined non-linear function, so we assumed a linear relationship for all indicators.
226 Supplementary Dataset 3 provides an overview of the relations we defined between each
227 indicator and ES.

228 Unique identifiers allowed us to define individual studies, regardless of whether they were
229 within a publication that included more than one study or across different publications
230 (Supplementary Methods 1). Multiple measures from within the same replicate site were
231 aggregated into a single value per replicate (see Supplementary Methods 1 for details).
232 Methods for standardizing measures of variance are presented in Supplementary Methods
233 4.

234 We obtained a final database with information on 457 ES indicators among 2,943 pairwise
235 comparisons of land covers from 133 studies. A log response ratio was used as the effect
236 measure for comparing pairs of land covers within each study, and was standardized such
237 that larger values always represented greater ES supply in the numerator land cover
238 relative to the denominator one (see Supplementary Methods 1 for this standardization
239 and log response ratio variance calculations).

240 Studies with more than one indicator of a given ES were aggregated to have the same
241 weight as studies with only a single indicator (this was based on either the mean log
242 response ratio across multiple indicators or the single indicator represented in all land
243 covers of a study, details in Supplementary Methods 1). Subsequently, the total number of
244 land cover comparisons in our final dataset of 133 studies was reduced from 2,943 to 920
245 comparisons for individual ES within single studies (See Supplementary Dataset 5 for an
246 overview of the final data).

247 **(2) Data analysis**

248 Data analysis was conducted as a two stage process: we first examined the supply of each
249 ES by different land covers, and then assessed the relationships among land covers in terms
250 of multiple ES. For the first stage, we conducted a separate network meta-analysis (Salanti,
251 2012) for each ES. While conventional meta-analysis compares 2 treatments at a time

252 (using direct comparisons from each study), a network meta-analysis can compare multiple
253 (i.e. 3 or more) treatments simultaneously. This is achieved by using both direct evidence
254 (studies comparing pairs of treatments) and indirect evidence derived from linking
255 common treatments across different studies in a network of evidence (Salanti, 2012). For
256 example, if some studies show that land cover A is better than B in supplying an ES, and
257 others provide direct evidence that B is better than C, then a network meta-analysis allows
258 us to make the inference that A will also be better than C. We therefore used network meta-
259 analysis to compare, for each ES, a wide array of land covers across different studies, even
260 though we did not have data for direct comparisons among all combinations of land covers.

261 We conducted our network meta-analyses with the R package *Netmeta* (Schwarzer *et al.*,
262 2019), which offers a frequentist approach to calculate point estimates (and their
263 corresponding 95% confidence intervals) of the effect of the different land covers on the
264 supply of individual ES. Estimates were expressed as the log response ratio of each land
265 cover relative to a reference land cover: high producing exotic grassland. We selected this
266 land cover as our reference, because it was the only land cover that was represented across
267 all ES in our dataset (and would therefore allow us to compare our results across ES at a
268 later stage).

269 In *Netmeta*, we used a random effects meta-analytic model to generate estimates and
270 confidence intervals from which we then calculated probability scores (*P*-scores; Rucker &
271 Schwarzer, 2015) on how different land covers ranked in the supply of each ES. Estimates,
272 confidence intervals and *P*-scores then allowed us to construct, for each ES, a so-called
273 forest plot or blobbogram (*sensu* Lewis & Clarke, 2001) to compare different land covers in
274 their ES supply.

275 Bundles, trade-offs and synergies in land cover effects across the whole suite of ES were
276 then examined using hierarchical clustering of the network meta-analytic estimates. For
277 this, we constructed a land cover by ES matrix (Fig. S44, Supplementary Results 3) using
278 the estimated log response ratios of each land cover (relative to the high producing exotic
279 grassland reference) in each ES, as determined with the individual network meta-analyses.

280 Missing values in this matrix resulted from sets of land covers for which we had no
281 information on a given ES or could not infer the corresponding ratios.

282 For analysis, we selected subsets of this matrix with no gaps and the largest possible
283 number of total cells. This resulted in two data subsets: a matrix of nine ES by eight land
284 covers and another matrix with nine land covers by eight ES. The matrix with nine ES was
285 rotated to have ES as rows (land covers as columns) and used to compare ES in terms of the
286 land covers that supply them. This allowed us to identify ES bundles (sets of ES supplied
287 similarly across multiple land covers), synergies in ES supply, and ES that would likely be
288 traded off with one another in land-use decisions. The matrix with nine land covers was
289 used to compare land covers (to identify redundancy) in the supply of eight ES. This
290 allowed us to explore how land-cover differences influence ES bundles.

291 We calculated a dissimilarity matrix from each of these matrices using the *daisy* function of
292 the *cluster* package for R (Maechler *et al.*, 2019) with Euclidean distances. For the rotated
293 matrix with nine ES, distances were based on ES observations for each land cover, while for
294 the matrix with nine land covers, distances were based on land cover observations for each
295 ES. We applied hierarchical clustering (using the R *hclust* function; R Core Team, 2019) to
296 each of the distance matrices and constructed dendrograms on how different land covers
297 or ES compared against each other. Following Raudsepp-Hearne *et al.* (2010), we also used
298 these distance matrices to conduct k-means cluster analysis (with the *kmeans* function in R;
299 R Core Team, 2019) and identify groups of land covers and ES exhibiting similar behavior.
300 In each case, the number of clusters was determined using a scree plot (Figs. S3 and S4,
301 Supplementary Methods 5).

302 Finally, we used our distance matrices with nine land covers to test hypotheses on whether
303 broad categories of land covers explained the trends observed in the corresponding
304 clustering. Specifically, land covers were grouped under two categorical variables, one
305 denoting the presence/absence of forest cover and another separating production land
306 covers, dominated by exotic vegetation cover, from those with no production activities.
307 Originally, we expected to compare land covers with a native vs. exotic vegetation cover
308 separately from production vs. no production. However, we omitted the former category

309 because, except for one, all land covers with exotic vegetation were production and all
310 native covers had little or no production. We used a permutational multivariate analysis of
311 variance (PERMANOVA) to test whether these variables or their interaction explained
312 between-land-cover differences in the supply of multiple ES.

313 PERMANOVA analyses were conducted using the *adonis* function of the *vegan* package in R
314 (Oksanen *et al.*, 2019). Variables are added sequentially in the *adonis* algorithm. To be
315 conservative, we performed the PERMANOVA twice and swapped the order of the variables
316 in the second iteration, so that each variable was tested second, after controlling for any
317 collinearity with the other predictor (i.e. adjusted sums of squares). The *betadisper*
318 function of the *vegan* package was used to test the assumption of multivariate homogeneity
319 of group dispersions, and all tests met this assumption. Table S4 (Supplementary Methods
320 5) presents the land cover categories used in these analyses.

321 **III. RESULTS**

322 **(1) Data coverage**

323 From our systematic survey, we identified a total of 133 studies that were relevant to our
324 analysis and matched our selection criteria. Overall, these studies contributed data on 17
325 different ES, 25 land cover types and 457 measures (which we term 'ES indicators') on ES
326 supply. All four of the Millennium Ecosystem Assessment ES categories (supporting,
327 provisioning, regulating and cultural services; MEA, 2005) were represented within our
328 dataset. However, most studies examined supporting and regulating services, with 115 and
329 110 studies, respectively. Only 44 studies presented data on provisioning services and four
330 on cultural ones. All of the ES in the supporting category (habitat provision, nutrient
331 cycling, soil formation, water cycling and primary production) are represented in our
332 database. Only four land cover comparisons had more than 20 studies (high producing
333 exotic grassland vs. exotic forest, indigenous forest vs. high producing exotic grassland,
334 short-rotation cropland vs. high producing exotic grassland and exotic forest vs. indigenous
335 forest); whereas the remaining land cover pairs were represented by 10 or fewer studies

336 each. Further details on the number of studies per land cover comparison and per
337 combination of ES and land cover are available in Supplementary Results 1.

338 **(2) Land cover effects on individual ES**

339 There were consistent trends in the supply of multiple services by specific land cover types,
340 but also great variability in the supply of some services. An overview of the evidence base
341 (number of studies, types of ES indicators and network of land cover comparisons) and the
342 outcomes of the individual network meta-analyses for each of the 17 ES in our database is
343 presented in Supplementary Results 2. In this supplement, we use forest plots (*sensu* Lewis
344 & Clarke, 2001), see Fig. S8, Supplementary Results 2 for an example) to show the main
345 results of the meta-analysis, i.e. how different land covers compare against each other in
346 their supply individual ES. Specifically, the values in these plots are given as log response
347 ratios which express the overall estimates of service supply by individual land covers
348 relative to a reference land cover (high-producing exotic grassland).

349 For several ES, the positive log response ratio estimate and narrow confidence intervals in
350 the forest plots (Figs. S8, S17, S19, S38, Supplementary Results 2) reveal that land covers
351 with native vegetation cover (i.e. broadleaved indigenous hardwoods, indigenous forest,
352 manuka/kanuka, matagouri or grey scrub and, in many cases, tall tussock grassland)
353 tended to rank higher in ES supply than the more intensive high-value production land
354 covers (particularly short-rotation cropland and high-producing exotic grassland).
355 Regulation of water timing and flows, water purification, freshwater provision and disease
356 mitigation conformed to this general pattern. In these services, low producing grasslands
357 (which comprise a mix of exotic and native vegetation) and exotic forests also perform
358 relatively well and always rank within the top half of all land covers.

359 For habitat provision (Fig. S13, Supplementary Results 2) the difference between land
360 covers with native vegetation and production systems was less important than the
361 presence of forest vegetation cover. For this service, most land covers with forest
362 vegetation (exotic forest, broadleaved indigenous hardwoods and indigenous forest)
363 ranked higher in their estimates of ES supply than those with open covers (short-rotation
364 cropland, tussock, low and high producing grasslands) or deciduous hardwoods.

365 Meanwhile, primary production tended to be highest under production systems (e.g.,
366 croplands, exotic forest, and high-intensity grassland) and lower in land covers with low or
367 no production (e.g., low producing and tussock grasslands, indigenous forest), rather than
368 differing between forested and open covers. However, these trends were not statistically
369 significant due to the wide and overlapping confidence intervals (Fig. S23, Supplementary
370 Results 2).

371 Importantly, these results indicate that no single land cover supplies all ES at a maximal
372 level. Indigenous forests ranked high in the supply of many ES (particularly habitat
373 provision, freshwater provision, disease mitigation and global climate regulation -
374 Supplementary Results 2). However, in some ES they were outperformed by other land
375 covers such as tall tussock grasslands (which were well suited to water purification; Fig.
376 S19, Supplementary Results 2) and advanced successional forest (broadleaved indigenous
377 hardwoods, which ranked high in regulation of water timing and flows, nutrient cycling and
378 habitat provision; Figs. S8, S11 and S13, Supplementary Results 2). Therefore, multiple land
379 covers will be required within the landscape to ensure the supply of multiple ES.

380 The forest plots in Supplementary Results 2 for primary production (Fig. S23), erosion
381 control (Fig. S27), pest regulation (Fig. S30), waste treatment (Fig. S32), capture fisheries
382 (Fig. S34), ethical & spiritual values (Fig. S36), pollination (Fig. S41) and regional & local
383 climate regulation (Fig. S43) all present wide, overlapping confidence intervals for all or
384 most of their estimates. This suggests statistically non-significant differences in the supply
385 of these services among land covers. For some services, this could be due to small evidence
386 bases, either in terms of few studies or few comparisons for specific land cover pairs within
387 the network of land cover comparisons that inform the meta-analysis. In the case of erosion
388 control, where the evidence base is formed by 22 studies (Supplementary Results 2 -
389 Erosion control), overlapping confidence intervals in the land covers with the greatest
390 number of comparisons (which would therefore be expected to have lower variance) still
391 expressed high variability in ES supply, suggesting that other factors besides land cover
392 (e.g., slope, soil type) likely account for the differences in erosion control across the sites in
393 all 22 studies.

394 **(3) Land cover effects across multiple ES**

395 We explored how the above trends in the supply of individual services translate into
396 bundles, synergies and trade-offs among ES. For this we conducted multivariate analyses to
397 simultaneously explore differences in the supply of multiple services across land covers
398 (see Methods - Data analysis). These analyses allowed us to examine whether groups of ES
399 responded similarly to differences in land cover and, conversely, whether groups of land
400 covers played a similar role in the supply of multiple ES.

401 *(a) Differences among ES from the land covers that supply them*

402 For this analysis we used a matrix of eight land covers by nine ES to identify clusters of ES
403 based on how they are supplied by different land covers. We identified a total of five
404 clusters, three of which were formed by only one ES while the remaining two had two and
405 four ES each (Fig. 1). This suggests that more than half of the nine ES in this analysis are
406 supplied in a distinct way by different land covers, and reinforces the notion that multiple
407 land covers are required to supply a range of ES. Moreover, the separation of services into
408 clusters of one to two also suggests that their supply is traded-off across land covers. This
409 trade-off is acute for water-related services; most of these tend to occupy distinct spaces
410 within the dendrogram, with water cycling standing apart from all other ES, water
411 purification and freshwater provision in a separate cluster, and regulation of water timing
412 and flows in a single branch close to global climate regulation and nutrient cycling (Fig. 1).
413 The trade-off between water cycling and regulation of water timing and flows is probably
414 because land covers that allow for increased runoff and present low water retention (such
415 as harvested forests, croplands and built-up areas) deliver more of the water cycling
416 service than land covers that promote soil water storage and, consequently, perform better
417 in regulating water timing and flows (e.g., broadleaved indigenous hardwoods, indigenous
418 forests and low producing grasslands). Freshwater provision and water purification form a
419 cluster because the water quality aspect of their supply was assessed with the same
420 indicators for both services (Supplementary Dataset 3) and, in both cases, greater service
421 supply came from land covers contributing to enhanced water quality (such as tall tussock
422 grassland and indigenous forest; Figs. S17 and S19, Supplementary Results 2).

423 In contrast to the water-related ES, those more closely linked to the soil system (nutrient
424 cycling and soil formation) are found closer to each other in Fig. 1, and appear to be
425 delivered similarly across land covers (Figs. S11 and S15, Supplementary Results 2). In our
426 analysis, global climate regulation falls under this broad group of services and is closely
427 linked to nutrient cycling (Fig. 1). This is likely due to the indicators shared by both
428 (Supplementary Dataset 3) and a gap in our database with respect to the contribution of
429 vegetation and livestock in greenhouse gas fluxes. In New Zealand, these contributions are
430 well studied within a given land cover, but the lack of comparisons across land covers and
431 uses prevented us from making a more comprehensive quantification of how this service is
432 supplied.

433 *(b) Differences among land covers in their supply of services*

434 Our analysis of how land covers compared against each other in their supply of ES was
435 based on a matrix of nine land covers by eight ES. We found a gradient of land covers that
436 separates those with lower production from the high value production systems (Fig. 2).
437 Land covers with high production value and dominated by exotic vegetation cover
438 (croplands, high producing exotic grassland, exotic and harvested forests) occupied
439 separate clusters from those with low or no production and primarily native components
440 in their vegetation cover (tall tussock and low producing grassland, manuka and/or kanuka
441 and indigenous forest). Likewise, with the exception of low producing grassland, land
442 covers with forest vegetation cover occupied separate clusters from those with a more
443 open vegetation cover.

444 The clusters with single land covers in Fig. 2 appear to specialize in supplying high levels of
445 only one to three of the nine ES used in the analysis. Tall tussock grassland supplies high
446 levels of water purification and freshwater provision, while manuka and/or kanuka (a
447 successional land cover) is noted for soil formation and regulation of water and timing of
448 flows; short-rotation cropland ranks high in supplying primary production. In contrast, the
449 three clusters with pairs of land covers in Fig. 2 exhibit a more uniform supply of the
450 different ES. Nevertheless, each of these three clusters also appears to supply a distinct ES
451 bundle. The cluster formed by exotic and harvested forests supplies a bundle with high

452 biomass production and habitat provision while the cluster formed by indigenous forest
453 and low producing grassland supplies a bundle specializing in purifying, providing and
454 regulating the flow of water. Lastly, the cluster formed by high producing exotic grassland
455 and orchard, vineyard and other perennial crops appears to supply even (yet not
456 necessarily high) levels of all ES.

457 Greater differences in ES supply can be inferred from the larger differences in the height at
458 which clusters separate from each other (Fig. 2). Consequently, in Fig. 2, the clusters with
459 two production land covers (harvested and exotic forest plus high producing exotic
460 grassland and orchard, vineyard & other perennial crops) are similar in their supply of ES
461 but differ from the cluster with indigenous forest and low producing grassland. In turn,
462 these three clusters with pairs of land covers are more similar to each other (indicated by
463 the lower branch point) than they are to the clusters with single land covers. The clusters
464 with pairs of land covers are also more close to the short-rotation cropland than to tall
465 tussock grassland and manuka and/or kanuka, which are more similar to each other than
466 they are to the rest of the land covers.

467 The trade-off in service supply between production and non-production land covers was
468 statistically significant (PERMANOVA, Pseudo $F_{1,6} = 3.064$, partial $R^2 = 0.312$, $p < 0.05$;
469 detailed results in Supplementary Results 4). The assumption of homogeneous dispersion
470 between both groups was met ($F_{1,8} = 0.718$, $p > 0.05$), suggesting that neither supplies a
471 greater range of ES among its different land covers. Conversely, the separation between
472 forested and non-forested land covers did not significantly explain the distribution of land
473 covers in ES space (Pseudo $F_{1,6} = 0.536$, partial $R^2 = 0.055$, $p > 0.05$; see also Supplementary
474 Results 4) nor did the interaction between forested/non-forested and production/non-
475 production (Pseudo $F_{1,6} = 1.159$, partial $R^2 = 0.118$, $p > 0.05$; Supplementary Results 4).

476 **IV. DISCUSSION**

477 We have synthesized over 40 years of quantitative primary evidence on the ES supplied by
478 different land cover types at a national scale, and used this to identify bundles and trade-
479 offs among ES, as well as general land cover characteristics driving these associations.
480 Overall, we found strong evidence that high-value production land covers supplied a

481 different set of non-market services than all the land covers with low or no production and
482 native elements in their vegetation cover. Together, land covers with low or no production
483 outperformed the production ones in supplying several supporting and regulating ES (e.g.,
484 freshwater provision, disease mitigation and regulation of water timing and flows). In
485 contrast, most production land covers specialized in supplying primary production.

486 Interestingly, forest cover (native or exotic) was not associated with significant differences
487 in the suite of services supplied. Instead, we observed a close affinity between land covers
488 with contrasting forest covers (e.g., between low producing grassland and indigenous
489 forest and between exotic forests and high producing exotic grasslands) in their supply of
490 several ES including water purification and regulation of water and timing of flows. Only
491 for habitat provision did we observe that land covers with a forest cover (indigenous forest
492 and exotic forest - harvested and unharvested) performed better than those without a
493 forest cover in service supply.

494 In New Zealand, production land covers are dominant, with exotic forests, high producing
495 exotic grasslands, croplands, and orchards/vineyards occupying 42% of the country's
496 terrestrial area in 2012 (Landcare Research, 2015). Our assessment, like other ES
497 assessments elsewhere (Costanza *et al.*, 2014), shows that decisions on ecosystem
498 management (such as those leading to the dominance of production land covers) reflect
499 preferences for a set of ES over others. Specifically, the trade-offs we find between
500 production and low or no production land covers illustrate how the preference for ES with
501 a high market value and short-term returns occurs at the expense of ES that have a non-
502 market value but are essential for sustained, long-term human well-being (Rodríguez-
503 Loinaz, Alday, & Onaindia, 2015).

504 The above findings resonate with the recommendations of Foley and colleagues (2011)
505 with respect to halting indiscriminate expansion of agriculture into sensitive ecosystems.
506 However, our findings also suggest that, at the landscape scale, the trade-offs between the
507 ES supplied by production and non-production land covers are not solved with a single
508 land cover. Even for the ES that were best delivered by land covers with no production, we
509 did not find evidence of a single land cover consistently performing better than the rest in

510 the supply of all ES. Therefore, a landscape with a mosaic of these land covers is more likely
511 to offer a broader suite of ES than one dominated by large extents of any single low or no
512 production land cover (Fischer, Lindenmayer, & Manning, 2006; Law *et al.*, 2015).

513 Thus, we support earlier recommendations to extend beyond the dichotomy of
514 conservation vs. production land into a more a comprehensive management (Grau,
515 Kuemmerle, & Macchi, 2013; Tschardtke *et al.*, 2005). Such management could, for
516 example, contemplate the extension or restoration of under-represented native land uses
517 at strategic sites where intensive use is not matched by increased production yield, to
518 promote the supply of critical ES or broaden the existing suite. To this end, management
519 will need to be informed by a comprehensive understanding of how ES can scale up from
520 individual land use units and how the relative sizes of different land use units within a
521 landscape can affect ES supply.

522 Our analysis shows that low-intensity production land covers that retain some native
523 vegetation (i.e. the low producing grasslands in our dataset) can approach native land
524 covers (indigenous forests) in terms of overall ES supply. These low-intensity production
525 land covers demonstrate that production and a suite of other ES can be jointly delivered,
526 providing empirical support to the notion of managed ecosystems with “restored” ES
527 proposed by Foley *et al.* (2005). Importantly, we identified great variability in how land
528 covers supplied certain ES, despite there being high replication in our evidence base for
529 these effects (e.g., erosion control by high producing exotic grasslands, indigenous and
530 exotic forests). This suggests that local environmental conditions (e.g., slope) and
531 management practices can significantly alter how a given land use affects ES supply
532 (Felipe-Lucia *et al.*, 2018). In turn, this implies some potential to improve ES supply by
533 adjusting management practices within specific land uses (Guerra & Pinto-Correia, 2016;
534 Pang *et al.*, 2017) or better incorporating local environmental conditions into land-use
535 decisions. Within individual land uses, decisions on which practices to adopt will require
536 detailed research on the effects of different management regimes on ES supply (Guerra &
537 Pinto-Correia, 2016; Maseyk, Dominati, & Mackay, 2018), as well as an understanding of
538 the extent to which the plasticity in ES supply is constrained (or favored) by environmental
539 factors.

540 A critical challenge in applying the ES framework to spatial and environmental planning is
541 understanding the extent to which different land uses affect ES supply (Braat & Groot,
542 2012). The uneven coverage of different ES that we observed in the literature reflects both
543 the variable difficulty of quantifying the supply for different ES and the likely relevance of
544 comparing the supply of certain ES among land uses. Within our dataset, supporting and
545 regulating ES are best represented. In the global literature, regulating ES are also the most
546 commonly quantified and mapped category, however, they are usually followed by
547 provisioning ES, while the evidence on supporting ES is scarce (Howe *et al.*, 2014; Malinga
548 *et al.*, 2015; Martínez-Harms & Balvanera, 2012; Crossman *et al.*, 2013). The limited
549 representation of provisioning ES in our dataset possibly occurred because most
550 provisioning ES (e.g., milk, timber) are linked to single or few land covers and,
551 consequently, are unlikely to be compared across land covers. Such services, however,
552 enter the market directly and can be more readily quantified in monetary terms. In
553 contrast, the supporting and regulating ES that predominate in our dataset usually
554 translate to externalities in the context of production systems, and are likely more readily
555 quantified through biophysical indicators than monetary units (Howe *et al.*, 2014; Czúcz *et*
556 *al.*, 2018).

557 Cultural ES are poorly represented in our database, with the few indicators for this
558 category all being shared with the capture fisheries provisioning service, because they
559 pertain to eels, which are of cultural significance to Māori in New Zealand. Cultural ES have
560 non-material and ideological dimensions that are not readily quantified and, thus, are not
561 well represented even within the emerging body of specialized literature on ES supply
562 assessment (Hernández-Morcillo, Plieninger, & Bieling, 2013). Moreover, it has been
563 suggested that cultural ES escape the instrumental value domain present in the ES
564 framework. Instead, they fall under the relational domain, whereby value is not solely
565 defined in terms of the direct benefits derived from an ecosystem, but also in terms of the
566 social webs of desired and actual relationships constructed around that ecosystem or its
567 components (Chan *et al.*, 2016). Consequently, for these ES, a quantitative approach like
568 ours should be complemented with assessments that address the relational dimensions of

569 the values people hold for the natural elements in different land uses to better represent
570 their importance in a cultural context (Lyver *et al.*, 2017).

571 Individual ES are defined to encompass distinct processes and values, but these are often
572 quantified by overlapping sets of indicators (Czúcz *et al.*, 2018). For example, in our dataset
573 indicators from water and soil pertained to more than one ES (e.g., water purification and
574 provision of freshwater both share indicators of water quality, while erosion control and
575 soil formation share indicators on soil stability). Ecosystem service indicators can also
576 occupy different positions in the spectrum connecting the supply and demand end of ES
577 (Villamagna, Angermeier, & Bennett, 2013). Here we have focused exclusively on the
578 supply end and, more specifically, on the capacity of land covers to provide ES rather than
579 on their actual flow or delivery as benefits perceived by a specific group of individuals.

580 Since the Millennium Ecosystem Assessment was released, there have been initiatives to
581 redefine ES and their categories (TEEB, 2010; CICES, 2018). Here we argue that future
582 work in determining how to best quantify ES, their potential and realized delivery, and
583 their spatio-temporal variation, will be at least as important as refining their taxonomy.
584 Furthermore, if a focus on quantifying ES should reveal aspects of services that are best left
585 unquantified (such as the relational domain of cultural ES), this could also lead to the
586 development of alternative ways of assessing those ES, which could then be applied in
587 combination with quantitative approaches like the one we have developed here. Recent
588 developments, like the concept of nature's contributions to people and the framework for
589 their assessment proposed by Díaz and colleagues (2018), provide an opportunity for
590 reconciling these issues.

591 Our work suggests that there is great potential in using existing data for assessing ES
592 bundles and interactions more cost-efficiently than through direct field observation. Yet, an
593 important caveat to our approach stems from underlying factors that are correlated with
594 land use and impact the supply of certain ES. For example, since land uses such as forestry
595 and natural habitats are frequently found on steep slopes, this physical characteristic will
596 likely influence erosion control in a way that co-varies with land cover. At the most extreme
597 end, some ES may not be related to land cover, but rather respond to other spatially

598 variable factors (e.g., aesthetic values from housing location on hillsides). These factors
599 were beyond the scope of our work, as we did not separate the effects of spatial factors
600 from those of land cover. In fact, one could argue that land use is not selected
601 independently from the local environment, so these factors are a frequent (though not
602 universal) component of any land use and its influence on ES. Nevertheless, future
603 approaches may benefit from examining how these factors affect the between- or within-
604 land-use differences in ES supply. This distinction would allow a shift from comparisons
605 across locations (as we examined here), which allow comparisons of existing landscapes, to
606 the predicted impacts of land use change on ES at any location. However, such predictions
607 would also need to incorporate legacy effects of past land uses, as these can have enduring
608 consequences on ecosystem functioning (Dallimer *et al.*, 2015; Perring *et al.*, 2016).

609 Our method for using existing data to assess bundles, trade-offs and synergies in ES supply
610 across land covers can facilitate the comparison of entire landscapes, for example, by
611 projecting land covers or land uses into multidimensional ES-supply space (Fig. 3). This
612 mapping could reveal two key characteristics for land-use planning: 1) land covers/uses
613 that cluster together, and thus exhibit redundancy (and potentially resilience) in ES supply,
614 or 2) land covers/uses that occur at opposite extremes of ES-supply space, and are
615 therefore likely to exhibit complementary roles in their service supply (as ES are traded off
616 between them). In addition, the total hyper-volume occupied by all land covers/uses in this
617 multidimensional ES-supply space (ordination plots in Fig. 3) can indicate the diversity of
618 ES supplied by all land covers/uses within a given landscape (analogous to interpretations
619 of species in trait space; Laliberte & Legendre, 2010), which could be used in comparisons
620 of existing landscapes or future scenarios.

621 For example, Case 3 in Fig. 3, has the greatest diversity of land covers and thus occupies the
622 greatest hyper-volume in multidimensional ES-supply space. However, there are few land
623 covers at the edge of this volume, such that the full array of services has low redundancy
624 compared with Case 2 where land covers cluster around one location in ES-supply space.
625 Because the entire ES-supply space may include areas that do not correspond to any
626 configuration of ES, this approach is best applied for comparing landscapes rather than as
627 an absolute measure of ES in one location.

628 Finally, mapping ES in multidimensional land-cover or land-use space (e.g., Fig. 1) allows
629 the identification of ES bundles that respond similarly to land cover / land use. These
630 bundles can then be used to identify management decisions that minimize disruption of
631 service flows. Our approach opens the way for actively incorporating existing sources of
632 information into ES research and informing practitioners to shape land systems that
633 sustainably support human well-being.

634 **V. CONCLUSIONS**

635 (1) Our synthesis of land cover supply of ES in New Zealand revealed a consistent trade-
636 off in the services supplied by high-value production land covers vs. those with low or
637 no production and native elements in their vegetation cover. While production land
638 covers specialized in the supply of primary production, low or no production land
639 covers supplied a broad array of supporting and regulating ES. We did not find any
640 evidence that forest cover was associated with any distinct patterns of ES supply.

641 (2) We show that the trade-off between ES supplied by production and non-production
642 land covers is not solved with a single land cover. In contrast to earlier suggestions
643 that a single natural ecosystem can support multiple ES at high levels (Foley *et al.*,
644 2005), our analyses reveal that a mosaic of different land covers will be required to
645 supply multiple ES within a landscape.

646 (3) We show that exploring how different land covers map on to multidimensional ES
647 space allows for an assessment of how diverse and resilient different combinations of
648 land covers can be in their supply of ES. Such assessments can effectively support land
649 use planning decisions beyond considerations of the specific identity of each land
650 cover and the ES it supplies.

651 (4) Our work suggests that there is great potential in using existing data for assessing ES
652 bundles and interactions more cost-efficiently than through direct field observation.
653 However, we also find that effective landscape management of ES will require further
654 research on how environmental and land management factors can mediate the effects
655 of land use on ES supply. We anticipate that these effects will differ across ES and will

656 be more pronounced for ES where there is high variability in the supply by individual
657 land covers (e.g., erosion control in our dataset).

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671 **VII. AUTHOR CONTRIBUTIONS**

672 JMT, EGB and CGC conceived and developed the original project concept; JMT and EGB
673 secured the funding for the project; all authors contributed to the study design; data was
674 acquired by CGC, with input from JMT and EGB; CGC, JMT, SN and ML contributed to the
675 data analysis; CGC drafted the manuscript; JMT, SN, ML and EGB made revisions and critical
676 appraisals of the manuscript.

677 **VIII. REFERENCES**

678 *References marked with asterisk have been cited within the supporting information.*

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906 **IX. SUPPORTING INFORMATION**

907 Additional supporting information may be found online in the Supporting Information
908 section at the end of the article.

909 **Supplementary Methods 1.** Detailed data collection and processing methods.

910 **Supplementary Methods 2.** Full search phrase for pilot and formal searches.

911 **Supplementary Methods 3.** Decision tree for full-text assessment.

912 **Supplementary Methods 4.** Conversion of confidence intervals to variance and
913 imputation of missing values.

914 **Supplementary Methods 5.** Scree plots and land cover classification for multivariate
915 analyses.

916 **Supplementary Results 1.** Overview of research effort for New Zealand.

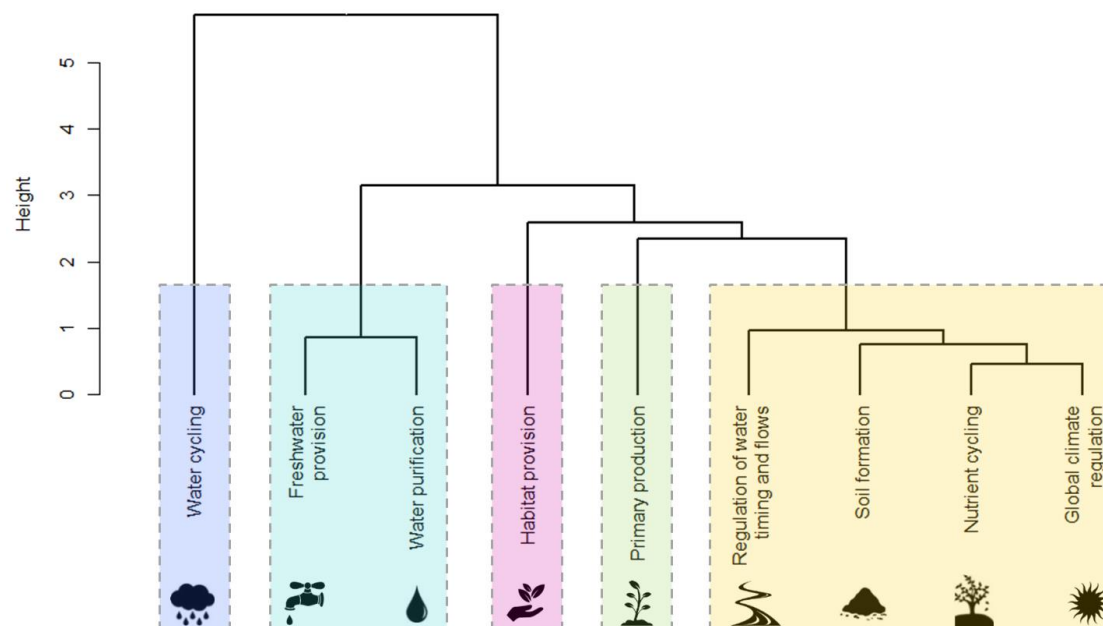
917 **Supplementary Results 2.** Evidence base and network meta-analysis for individual ES.

918 **Supplementary Results 3.** Summary of log response ratios per land cover and ecosystem

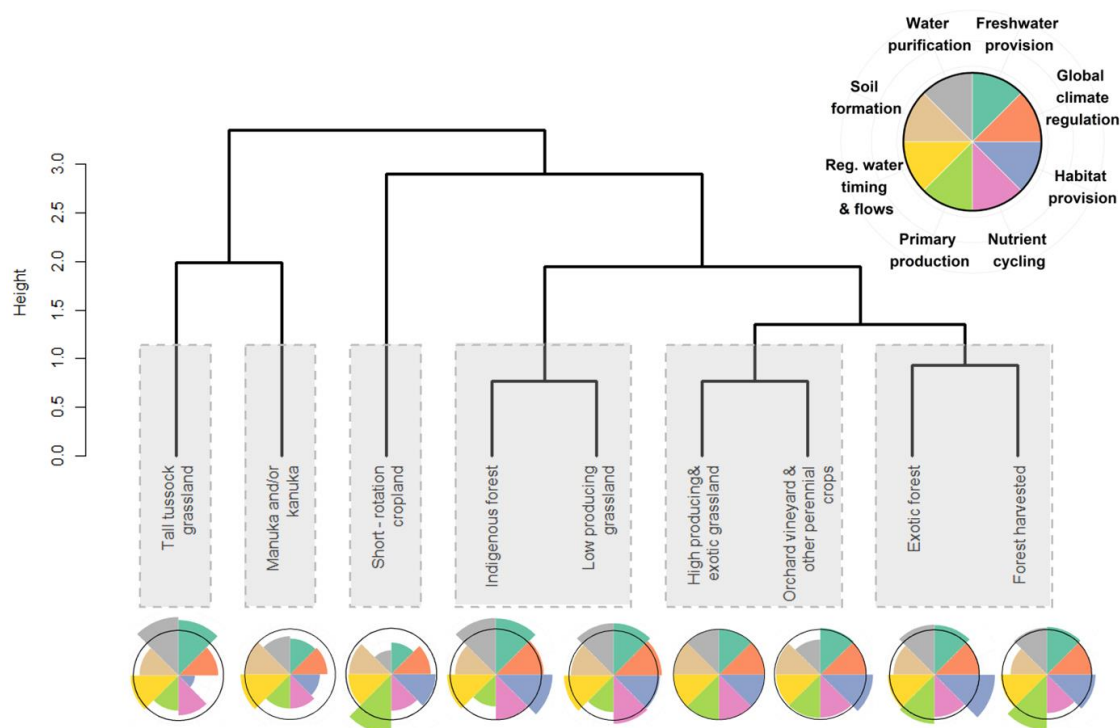
- 919 service combination.
- 920 **Supplementary Results 4.** Detailed results from PERMANOVA analyses.
- 921 **Supplementary Results 5.** Data analysis with allocation of a single ES to each indicator.
- 922 **Supplementary Dataset 1.** Overview of Ecosystem Services (ES).
- 923 **Supplementary Dataset 2.** Overview of land cover classes as defined in New Zealand's
- 924 Land Cover Database (LCDB).
- 925 **Supplementary Dataset 3.** Quantitative indicators used to quantify supply of each
- 926 ecosystem service.
- 927 **Supplementary Dataset 4.** Reference list for the studies included in our meta-analysis.
- 928 **Supplementary Dataset 5** Final log Response Ratios on ecosystem service supply for
- 929 pairwise comparison of land covers in each study used in our analysis.

1 FIGURES

2



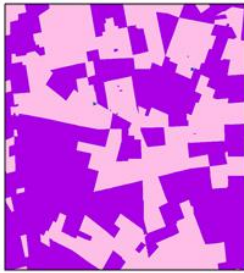
4 **Fig. 1: Hierarchical clustering of ES.** Services within the same box form a cluster (as
5 determined by k-means cluster analysis) and are therefore supplied similarly across eight
6 land covers (low producing grassland, tall tussock grassland, high producing exotic grassland,
7 short - rotation cropland, indigenous forest, exotic forest, harvested forest and orchard,
8 vineyard and other perennial crops). A greater separation between the branching points for
9 clusters along the height axis indicates greater dissimilarity among clusters in the extent to
10 which they are supplied by the eight land covers included in the analysis.



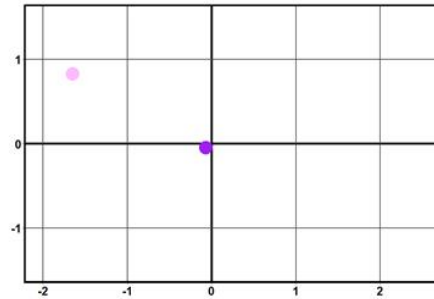
11

12 **Fig. 2: Hierarchical clustering of land covers.** Boxes enclose land covers that exhibit a
 13 greater similarity in their supply of eight ecosystem services (habitat provision, primary
 14 production, freshwater provision, soil formation, nutrient cycling, water purification, global
 15 climate regulation and regulation of water timing and flows). In contrast, land covers that
 16 merge at a greater height have a greater dissimilarity in their service supply. The flower
 17 diagrams at the bottom illustrate how each land cover supplies each of the eight ES, with
 18 longer petals indicating a greater supply of an ES. For comparison, the black ring around
 19 each flower diagram marks the supply from high producing exotic grassland, the land cover
 20 used as reference in our meta-analysis.

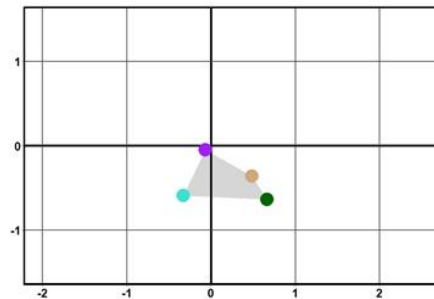
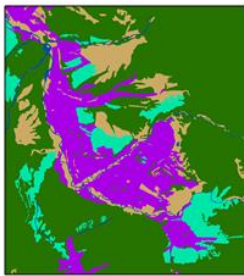
Case 1



"Ecosystem services space"



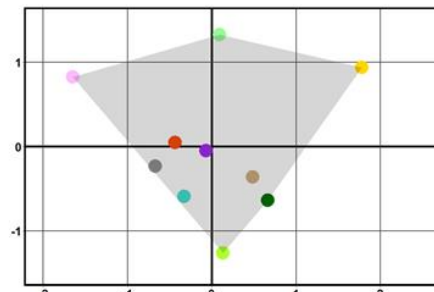
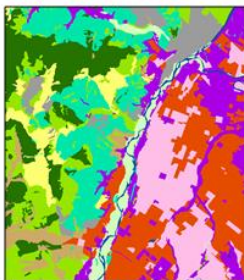
Case 2



Land covers

- Broadleaved indigenous hardwoods
- Exotic forest
- Forest harvested
- High producing exotic grassland
- Indigenous forest
- Low producing grassland
- Manuka and/or kanuka
- Orchard, vineyard & other perennial crops
- Short - rotation cropland
- Tall tussock grassland

Case 3



21

22 *Fig. 3: Example visualizations for exploring land cover trade-offs in the supply of*
23 *multiple ecosystem services (ES) from entire landscapes. Quantitative measures of ES*
24 *supply by different land uses or land covers (such as those obtained from our meta-analysis)*
25 *can be used to generate ordinations that 'map' land covers or land uses into the*
26 *multidimensional space of ES supply (ordination graphs). Distribution of land covers within*
27 *that space can assist with identification of redundancies in ES supply (among land*
28 *covers/uses that map close together) and trade-offs among land covers/uses that supply*
29 *contrasting sets of ES and, consequently, occupy opposite extremes of the ordination space.*
30 *Furthermore, the hypervolume enclosed by the total set of land covers/uses from a given*

31 *landscape expresses the diversity of ES provided by that landscape. As an example, our data*
32 *can be used to compare multi-service provision for: a landscape with few, undifferentiated*
33 *production land covers (Case 1); a landscape with a combination of some production and non-*
34 *production land covers (Case 2) and a landscape with a broad range of production and non-*
35 *production land covers that supply a diverse range of services (Case 3).*

36