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1 The interplay of landscape composition and configuration: new pathways to manage
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124 Abstract

125 Managing agricultural landscapes to support biodiversity and ecosystem services are key aims
126 of a sustainable agriculture. However, how the spatial arrangement of crop fields and other
127 habitats in landscapes impacts arthropods and their functions is poorly known. Synthesizing
128 data from 49 studies (1,515 landscapes) across Europe, we examined effects of landscape
129 composition (% habitats) and configuration (edge density) on arthropods in fields and their
130 margins, pest control, pollination and yields. Configuration effects interacted with proportions
131 of crop and non-crop habitats, and species' dietary, dispersal and overwintering traits led to
132 contrasting responses to landscape variables. Overall, however, in landscapes with high edge
133 density, 70% of pollinator and 44% of natural enemy species reached highest abundances and
134 pollination and pest control improved 1.7 and 1.4-fold, respectively. Arable-dominated
135 landscapes with high edge densities achieved high yields. This suggests that enhancing edge
136 density in European agroecosystems can promote functional biodiversity and yield-enhancing
137 ecosystem services.

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146 INTRODUCTION

147 Worldwide, intensive agriculture threatens biodiversity and biodiversity-related ecosystem
148 services (Foley *et al.* 2005). At a local field scale, monocultures and pesticides restrict many
149 arthropods and plants to non-cropped areas (Geiger *et al.* 2010). Thus, the majority of
150 organisms that provide key regulating services to agriculture, such as pollination and natural
151 pest control, must colonize fields from non-cropped, semi-natural areas (e.g. road verges,
152 grass margins, hedgerows, fallows), neighboring fields or in the wider landscape (Blitzer *et*
153 *al.* 2012). Semi-natural habitats, however, are often removed to facilitate the use of modern
154 machinery or converted to crops to increase production (Naylor & Ehrlich 1997), resulting in
155 reduced populations of service providing organisms (Holland *et al.* 2016). Consequently, the
156 sustainability of modern food production is increasingly questioned (Garnett *et al.* 2013).

157 ‘Ecological intensification’ has the potential to enhance the sustainability of agricultural
158 production by increasing the benefits agriculture derives from ecosystem services (Bommarco
159 *et al.* 2013). Supporting populations of ecosystem service providers is a key component of
160 ecological intensification (Bommarco *et al.* 2013). However, we currently lack detailed
161 knowledge on the landscape-scale management choices needed to achieve ecological
162 intensification with a high degree of certainty (Kleijn *et al.* 2019). For example, semi-natural
163 habitats are prerequisite for many organisms, but effects are often taxon-specific. In addition,
164 the presence or abundance of functional groups of organisms in a landscape does not always
165 correlate with the services they provide to crops (Tscharntke *et al.* 2016; Karp *et al.* 2018).

166 The configuration of landscapes (size, shape and spatial arrangement of land-use patches), in
167 addition to their composition (proportion of land-use types), is increasingly suggested as a key
168 factor in determining biodiversity and associated ecosystem services in agricultural
169 landscapes (Fahrig 2013). However, studies have only begun to disentangle the relative roles

170 of the composition *vs.* the configuration of habitats and fields within landscapes (Fig. 1;
171 Fahrig 2013; Haddad *et al.* 2017). Landscape configuration can be measured as the density of
172 edges between crop fields and their surroundings, including neighboring crops and non-crop
173 areas. Complex landscapes where small and/or irregularly shaped fields and habitat patches
174 prevail have a high density of edges. Due to increased opportunities for exchange, these
175 landscapes are likely to support spillover of dispersal-limited populations between patches
176 (Smith *et al.* 2014; Fahrig 2017). This may enhance populations' survival in the face of
177 disturbance and their potential to provide services in crops (Boetzl *et al.* 2019). Further, if
178 landscapes with high edge density are also spatially and temporally diverse in their
179 composition, organisms in these landscapes may benefit from landscape-scale resource
180 complementation and supplementation (Dunning *et al.* 1992). In this context, areas offering
181 refuges or complementary food resources may encompass uncropped (semi-natural) areas, but
182 also neighboring crops with asynchronous phenology, different host species and/or variable
183 timing and intensity of management interventions (Vasseur *et al.* 2013; Schellhorn *et al.*
184 2015). However, previous studies have found contrasting effects of increasing configurational
185 complexity for different taxa (Concepción *et al.* 2012; Plečáš *et al.* 2014; Duflot *et al.* 2015;
186 Fahrig *et al.* 2015; Gámez-Virués *et al.* 2015; Perović *et al.* 2015; Martin *et al.* 2016; Bosem
187 Baillod *et al.* 2017; Hass *et al.* 2018). Thus, there is currently no consensus on the importance
188 of landscape configuration for arthropods and the services they provide in crops (Seppelt *et*
189 *al.* 2016; Perović *et al.* 2018). Further, interactions between landscape composition and
190 configuration might explain seemingly contradictory results, but have rarely been tested in
191 part due to a lack of independent landscape gradients (but see Coudrain *et al.* 2014; Bosem
192 Baillod *et al.* 2017).

193 Species' responses to environmental filters depend on sets of biological traits ('response
194 traits'), such as diet breadth and dispersal ability, that constrain species' reactions to

195 environmental predictors (Lavorel & Garnier 2002). The resulting filtering of ecological
196 communities determines the presence or abundance of arthropods able to provide ecosystem
197 services (Gámez-Virués *et al.* 2015). Organisms with similar responses to environmental
198 filters may share specific combinations of response traits, known as trait syndromes.
199 Characterizing these syndromes and their responses to landscape gradients is critical to
200 predict the consequences of land-use change for biological communities (Mouillot *et al.*
201 2013) and the services they provide. However, trait-based responses of arthropods in cropland
202 to landscape gradients have only recently been investigated (Bartomeus *et al.* 2018; Perović *et*
203 *al.* 2018) and cross-taxonomic approaches in agroecosystems are lacking (but see Gámez-
204 Virués *et al.* 2015). For pollinators, natural enemies and pests in agricultural landscapes, a
205 high diversity of responses due to trait variation within and between groups ('response
206 diversity') is likely to underlie observed abundance patterns. In turn, this may affect our
207 ability to manage landscapes for maximum abundance and/or effectiveness of crop ecosystem
208 service-providers, and for minimum impacts of pests.

209 Here, using data from 49 studies covering 1,515 European agricultural landscapes and more
210 than 15 crops, we aim to disentangle arthropod responses to landscape gradients and their
211 consequences for agricultural production by performing the first empirical quantitative
212 synthesis of the effects of landscape configuration (edge density) and composition (amount of
213 crop and semi-natural habitats) on arthropods and their services in cropland. We include
214 observations of the abundance of pollinators, pests and pests' natural enemies (predators and
215 parasitoids) sampled in fields and their margins, and measures of natural pest control,
216 pollination, and crop yields. We use landscape predictors calculated similarly for all studies
217 from high resolution maps with standard land use-land cover classification. We test the
218 following *predictions*:

219 1. *Within functional groups of pollinators, pests and natural enemies, responses to landscape*
220 *predictors differ among trait syndromes.* Thus, considering key trait syndromes of arthropods
221 should increase our ability to predict the effects of landscape variables on functional groups.
222 On one hand, species that use specific crop or non-crop resources should benefit from
223 increased proportions of these resources (habitats) in the landscape (Tscharntke *et al.* 2012).
224 On the other hand, species with medium to low dispersal ability and diet or habitat needs
225 outside crops should be most abundant in fields and margins of landscapes with high edge
226 density, due to shorter travel distances and/or greater resource complementation between
227 habitats and crops (Smith *et al.* 2014).

228 2. *Effects of landscape composition and configuration interact.* Increasing resources in
229 surrounding arable and semi-natural areas should support arthropods and arthropod-driven
230 services in crops most effectively when travel distances are short (edge density high),
231 promoting spillover between surrounding areas and crops. Further, short travel distances
232 promoting spillover may compensate for scarce arable or semi-natural resources.
233 Consequently, positive effects of edge density on abundance and services in crops may be
234 strongest at low amounts of non-crop habitat (Fig. 1; Holland *et al.* 2016).

235 3. *Effects of landscape variables on arthropods and services are hump-shaped across Europe*
236 *(Fig. 1d; Concepción et al. 2012).* Indeed, resource complementation may be optimal at
237 intermediate habitat amount, but insufficient at high amounts of crop or non-crop habitat
238 (Tscharntke *et al.* 2012). Similarly, edges may facilitate spillover at low to medium density,
239 but hinder dispersal at high edge density due to barrier effects (e.g. in the presence of hedges;
240 Wratten *et al.* 2003) or high spatiotemporal heterogeneity of the agricultural mosaic (Díaz &
241 Concepción 2016). Due to interactions (prediction 2), decreases in abundance or services at
242 extreme values of habitat amount may be lifted under conditions of high edge density, and
243 vice versa (shaded grey areas in Fig. 1d).

244 To date, interactive and non-linear effects of landscape variables on arthropods have rarely
245 been explored, and to our knowledge never in the context of trait-based responses to
246 landscape gradients. We test these predictions for a broad range of taxa and three production-
247 related ecosystem services. We show that the diversity of responses to landscape variables is
248 high among pollinators, enemies and pests, and effects of landscape composition and
249 configuration depend on each other. But overall, high landscape edge density benefitted a
250 large proportion of service-providing arthropods. It was also positive for service provision
251 and harmful for pests, indicating a landscape-scale solution for ecological intensification that
252 does not require setting-aside large amounts of arable land and comes with strong benefits for
253 arthropod functional diversity.

254

255 MATERIAL AND METHODS

256 *Data collection and collation*

257 Data holders were approached through networks of researchers with the aim of collecting raw
258 data from a representative sample of studies performed in European crops. After initial
259 collection, data were screened for missing countries or crops systems, and requests were
260 targeted at researchers having published in these areas. Of 77 proposed studies, 58 provided
261 data with sufficient site replication and high resolution land-use maps (Table S1, Appendices
262 S1, S2 in Supporting Information). Requested data were arthropod abundance per unit area
263 and time (species richness when available) and measures of pollination, pest control and
264 yields, sampled along gradients of landscape composition and configuration in ≥ 8 sites. Sites
265 included annual and perennial crop fields, managed grasslands, field margins and orchards.
266 Farms were conventional, low-input conventional or organic. Data were collated and
267 standardized as described in Appendix S1. After preliminary analyses, we excluded organic

268 sites because few studies compared conventional and organic farms in similar landscapes.
269 This led to a total of 49 studies and 1,637 site replicates from 1,515 distinct landscapes
270 (circular map sectors; Appendix S1, Fig. S1), some sites having been sampled in multiple
271 studies.

272 *Landscape variables*

273 We used land-use maps provided by data holders to calculate landscape variables for all
274 studies. First, we standardized map classification to five land-use classes (arable, forest, semi-
275 natural habitat, urban and water). Semi-natural habitat included hedges, grassy margins,
276 unmanaged grasslands, shrubs, fallows (Appendix S1). We then calculated variables in six
277 circular sectors of 0.1 to 3 km radius around sites (Appendix S1, Fig. S1). Several indices can
278 be used to describe landscape composition, including % arable land and % semi-natural
279 habitat (SNH) (e.g. Chaplin-Kramer *et al.* 2011). To test the importance of these land-use
280 classes, we selected % SNH and % arable land as measures of landscape composition and
281 used them in parallel sets of models to avoid collinearity (see Statistical analyses).

282 Similarly, several measures of landscape configuration exist. Among them, the density of
283 edges available for exchange between landscape patches theoretically underpins mechanisms
284 of spillover and resource complementarity for biodiversity and services (see Introduction),
285 and has been frequently used in other studies (e.g. Holzschuh *et al.* 2010; Concepción *et al.*
286 2012). We thus measured landscape configuration as the total length of edges per area of each
287 landscape sector (edge density ED, in km/ha) between crop fields and their surroundings.
288 Hereby, we consider the combined effects of crop / crop (between fields) and crop / non-crop
289 edges (Fig. 1). Both interfaces may enhance arthropod movements in and out of fields
290 (Schellhorn *et al.* 2015). At radii up to 0.5 km, ED is negatively related to mean field size and
291 positively to the density of edges per area of arable land (Fig. S2). Importantly, ED reflects

292 the grain of whole landscapes including non-crop elements and crops. Thus landscapes with
293 high ED have comparatively small fields and non-crop patches. A decrease in ED is related to
294 an increase in size of both field and/or non-crop patches, and reflects a lower total density of
295 edges available for exchange in the whole landscape.

296 *Functional groups and arthropod traits*

297 We classified above-ground arthropods into functional groups of pollinators, pests and natural
298 enemies of pests (Appendix S1, Table S2). Organisms that are predators or herbivores as
299 larvae, but pollinators as adults were classified according to the life stage sampled.

300 Arthropods that could not be classified into these groups (Appendix S1) were included in
301 analyses of total arthropod abundance, as they contribute to overall farmland biodiversity, but
302 not in separate analyses of pollinators, pests and natural enemies (see Statistical analyses).

303 Six categorical traits associated with dispersal mode, overwintering behavior and diet were
304 hypothesized to influence the response of arthropods to landscape variables, as they relate to
305 the need and/or ability to move or disperse between habitat types to access food, hosts,
306 nesting or overwintering resources (Table 1). We defined traits for all arthropod species or
307 families according to the availability of information on separate taxa and to dataset resolution
308 (Appendix S1, Table S2; 36 out of 58 datasets provided species-level identification). We used
309 hierarchical cluster regression to identify parsimonious combinations of shared traits for
310 organisms with shared responses to landscape filters (Appendix S1; Kleyer *et al.* 2012). These
311 combinations are defined as trait syndromes characterizing different responses of species
312 groups to the environment (see Introduction). As trait syndromes may vary according to the
313 functional group (Lavorel & Garnier 2002), we identified them separately for pollinators,
314 natural enemies and pests (Figs. S3, S4). Trait syndromes are defined parsimoniously based

315 on one or a few trait combinations. However, all traits contribute to whole syndrome
316 definition and are described in Figs. S3, S4.

317 *Statistical analyses*

318 We calculated arthropod abundance in each site at three nested levels of community structure
319 (all arthropods; pollinators, enemies and pests; trait syndromes within functional groups;
320 Appendix S1). Pest control, pollination and yields were available from a subset of studies
321 (Table S3). For this subset, we calculated an ecosystem service index representing the amount
322 of service provided (Appendix S1). We analyzed effects of landscape predictors on arthropod
323 abundance and services using linear mixed effects models in R package lme4 v.1.1-15 (Bates
324 et al. 2015). We focused on abundance because it has been found to drive ecosystem service
325 provision (Winfree *et al.* 2015). However, abundance and species richness were positively
326 related across groups (estimates of linear mixed models relating richness to abundance using
327 $\ln(x+1)$ -transformed data, with random intercept for study and year: 0.4 ± 0.01 , $p < 0.001$ for all
328 arthropods, pollinators and enemies). We $\ln(x+1)$ -transformed abundance and services to
329 meet assumptions of normality and homoscedasticity. Predictors were % SNH and % arable
330 land as measures of landscape composition, and edge density as measure of configuration. We
331 expected changes at low values of predictors to have more impact than at high values, thus we
332 $\ln(x+1)$ -transformed the predictors. This transformation improved model fits (R^2 , see below)
333 and was maintained for all analyses.

334 To account for collinearity of composition variables (Fig. S2), we performed two sets of
335 models including either % SNH or % arable. Correlations between edge density and
336 composition variables were low within and across studies (Fig. S2; mean within-study
337 Spearman rho 0.05, SD 0.2, mean variance inflation factor of models with all arthropods 2.7,
338 SD 1.8), but some studies showed high correlation in specific years and scales (Table S4). We

339 thus ran analyses including and excluding these studies. As no differences were found in
340 overall results, we present analyses including all studies (Appendix S1).

341 Full models took into account hypotheses of a) interactions between landscape variables, and
342 b) non-linearity by including quadratic model terms (Appendix S1). To reflect the ranges
343 covered by European landscape gradients, we did not standardize landscape predictors within
344 studies. In this way we were able to capture non-linear effects across full gradients, i.e. that
345 responses to landscape change within studies may differ across full European gradients in
346 landscape composition and configuration (Van de Pol & Wright 2009). For comparison, we
347 evaluate effects using i) landscape variables mean-centered within studies and ii) standardized
348 response variables in Appendix S3.

349 We accounted for the data's hierarchical structure by including random effects for study and
350 year, sampling method and block (Appendix S1), and scaled predictors across studies by
351 mean-centering and dividing them by two standard deviations (R package arm v.1.9-3,
352 Gelman & Su 2016). We ran separate models at successive scales of 0.1, 0.25, 0.5, 1, 2 and 3
353 km radius around fields. Results at all scales (estimates and boot-strapped 95% confidence
354 intervals [CI] of full models) are presented Figs. S5-7. Figs. 2-4 illustrate results at 1 km
355 radius. We calculated R^2 of the models as the variance explained by fixed (marginal R^2 , R^2_m),
356 and by fixed and random terms (conditional R^2 , R^2_c), respectively (Nakagawa & Schielzeth
357 2013). Successive spatial scales are inherently correlated, and results at one scale are likely to
358 be reflected at other scales (Martin *et al.* 2016). In results, we focus interpretation on effects
359 that were significant (CI do not overlap zero) at more than one scale, as these indicate
360 robustness across scales and have the broadest implications for landscape management
361 (Pascual-Hortal & Saura 2007).

362 Few studies sampled all taxa and services in the same sites. To avoid lack of common support
363 for contrasts (e.g. a functional group sampled only in a portion of the overall gradient;
364 Hainmueller *et al.* 2018), we performed separate models for each functional group and
365 service. Replicate numbers for all responses and sites are provided in Tables S5, S6. Residual
366 normality and homoscedasticity were validated graphically. We verified the absence of
367 residual spatial autocorrelation using spline correlograms across studies (Zuur *et al.* 2009).
368 Statistical analyses were performed in R Statistical Software v. 3.4.1 (R Core Team 2017).

369

370 RESULTS

371 *Abundance of arthropods and functional groups*

372 We synthesized effects of landscape predictors on the abundance of 132 arthropod families,
373 encompassing over 494,120 individuals and 1,711 identified species or morphospecies. Of
374 these individuals, 50%, 10% and 37% were classified as natural enemies, pollinators and
375 pests, respectively (44%, 33% and 1% of species; Table S2). Effects of % SNH on arthropod
376 abundance were convex at high edge density (Figs. 2, S5). Effects of edge density depended
377 on % SNH, and led to a 2-fold increase at high (>20%) and 1.6-fold increase at low (<2%)
378 SNH. However, in landscapes with low edge density, increasing % SNH had no effect on
379 arthropod abundance.

380 Pollinators, natural enemies and pests showed distinct patterns when considered separately
381 (Fig. 2). Pollinators showed a similar convex effect of % SNH and a negative effect of %
382 arable land (Fig. S5), but effects were scarce on all natural enemies or all pests. The
383 conditional R^2 of these models was high (mean maximal R^2_c across scales 0.80, SD 0.06), but
384 the variance explained by landscape predictors was low (mean maximal R^2_m across scales

385 0.04, SD 0.03). However, breaking up these groups into trait syndromes led to further
386 differentiation and a clearer picture.

387 *Trait syndromes of enemies, pollinators and pests*

388 Trait syndromes obtained by cluster regression varied between enemies, pollinators and pests,
389 with the most clusters identified among natural enemies (Figs. S3-4). Though scarce overall,
390 effects of landscape predictors on enemies were significant across scales and highly
391 contrasted between trait syndromes (Fig. 3a, S6). Three main patterns emerged: 1) Enemies
392 overwintering outside crops, including flight and ground-dispersers (327 species, 44% of
393 enemies), benefited from high edge density. This was especially true in landscapes with <10%
394 SNH for flyers, and <60% arable land for ground-dispersers (Fig. 3a, S6). These groups
395 increased with increasing % SNH and decreasing % arable land, but effects depended on edge
396 density: they occurred at low (flight) or high edge density (ground-dispersers). 2) In contrast,
397 enemies able to overwinter in crops were most abundant in landscapes with few edges (Fig.
398 3a, S6). Among these, ground-dispersers benefited from high % arable land, but flyers
399 benefited from high % SNH. 3) Effects of landscape predictors on wind-dispersers, mainly
400 ballooning spiders and parasitoid wasps (flight/wind), were scarce.

401 Different responses also emerged among pollinators. Similarly to all arthropods, non-
402 agricultural specialist pollinators increased with high edge density at high or low % SNH
403 (Fig. 3b, S6; 393 species, 70% of pollinators). In contrast, agricultural specialists (e.g.
404 aphidophagous syrphids) were most abundant in landscapes with few edges and high % arable
405 land.

406 Pests able to overwinter in crops showed few effects of landscape variables across scales. But
407 pests considered to leave crops over winter were six times less abundant in landscapes with
408 high edge density (0.2-0.4 km/ha), regardless of their composition (Fig 3c, S6). Due to an

409 increase beyond this range at intermediate % SNH, 0.2-0.4 km/ha of edges represented an
410 area of minimum pest density along the observed gradients.

411 Marginal R^2 of models including trait syndromes averaged 0.11, SD 0.07 (mean maximal R^2 _m
412 across scales). Thereby, landscape predictors had significantly higher explanatory power
413 when applied to trait syndromes within functional groups, than to whole groups of natural
414 enemies, pollinators and pests (Wilcoxon rank sum test, $W=1289$, $p<0.001$).

415 *Pest control, pollination and yields*

416 Pest control, pollination and yields are given for a subset of studies (Tables S3, S6; Figs. 4,
417 S7). Pest control by natural enemies was highest in landscapes with low % arable land
418 (<40%) and high edge density, where it increased 1.4-fold compared to landscapes with low
419 edge density. It was lowest in coarse-grained landscapes (low edge density) with either low or
420 high % arable land (Fig. 4a). Pollination increased with edge density: it was 1.7 times higher
421 in fine-grained compared to coarse-grained landscapes regardless of % SNH or % arable land.
422 Low pollination was observed in landscapes with >70% arable land and at edge densities <0.1
423 km/ha (Fig. 4b right panel). Yields showed a variable pattern (Fig. 4c, S7). They were highest
424 in landscapes with 10-20% SNH at high edge density (Fig. 4c left panel). Lowest yields were
425 achieved in landscapes with <40% arable land and high edge density (Fig. 4c right panel). In a
426 range of landscapes including a large range of edge density and % arable land, intermediate to
427 high yields were maintained. The variance explained by landscape predictors in models of
428 pest control, pollination and yields averaged 0.14, SD 0.08 (mean maximal R^2 _m across scales;
429 mean maximal R^2 _c 0.60, SD 0.09).

430 Additional analyses show that effects occurred mainly across full gradients instead of within
431 standardized landscape ranges and were robust to standardization of response variables
432 (Appendix S3), as well as to the analytical method chosen (Appendix S4).

433

434 DISCUSSION

435 This synthesis shows that the response of arthropod abundance and services to landscape
436 predictors is non-linear across Europe and depends on interactions between landscape
437 composition and configuration, and on the response traits of arthropods. Overall, arthropods
438 were most abundant in landscapes that combine high edge density with high proportions of
439 semi-natural habitat. Functional groups of pollinators, enemies and pests did not strongly
440 reflect this pattern. Rather, trait syndromes within groups showed contrasting trends.

441 Pollinators that do not feed on pests or crops as larvae (non-pest butterflies, non-
442 aphidophagous syrphids, bees), and flying and ground-dwelling enemies considered to
443 overwinter mainly outside crops, benefited from high edge density at low or high habitat
444 amount and may require a high density of ecotones as exchange interfaces in order to
445 spillover between and into crops (Concepción *et al.* 2012; Tschardt *et al.* 2012; Hass *et al.*
446 2018). For organisms with limited dispersal ability, this requirement is likely due to the need
447 to recolonize crops in spring. However, the same driver affected strong aerial dispersers such
448 as wasps and butterflies, for which it may be more related to a high sensitivity to disturbance
449 within fields, and/or to the need for resource complementation through a high diversity of
450 available plants and prey (Sutter *et al.* 2017) or nesting sites. Such diverse resources can be
451 found in neighboring semi-natural habitats (e.g. nest sites; Holland *et al.* 2016), but also in
452 adjoining crops (pollen and nectar from crops and weeds, host plants or prey for herbivores
453 and predators). Indeed, a high number of separate field units is the first requirement to support
454 a high diversity of arable crops at organism-relevant scales. Landscapes with high vs. low
455 edge density may also differ in their crop composition and/or diversity, with associated
456 impacts on the arthropod community.

457 In contrast, ground-dispersing enemies with generalist overwintering needs, and pollinators
458 whose larvae feed on crops or pests, were most abundant in landscapes with few edges and
459 high % arable land. These groups benefit from agricultural resources and were able to
460 maintain populations in coarse-grained landscapes with high % arable land that other
461 organisms avoided. They thus represent important insurance organisms contributing to
462 arthropod response diversity (Cariveau *et al.* 2013), and may continue to provide services in
463 coarse-grained landscapes with little non-crop habitat (Rader *et al.* 2016; but see Stavert *et al.*
464 2017). However, abundances were too low for these trends to be reflected in overall patterns.
465 In addition, pests also benefited from landscapes with low edge density. The services
466 provided by agriculture-resilient enemies and pollinators are thus likely insufficient to balance
467 the bottom-up effects of high crop resource availability on pests in such low complexity
468 landscapes (Walker & Jones 2003).

469 Pests overwintering outside crops were least abundant, and pollination and pest control were
470 highest, in landscapes with high edge density, particularly within the range of 0.2-0.4 km/ha.
471 In agreement with Rusch *et al.* (2016), pest control was also highest at low % arable land. But
472 for pests and pollination, edge density effects occurred largely independently of landscape
473 composition. Based on trait syndrome patterns, pest control and pollination appear to have
474 been largely driven by organisms without strong links to agricultural resources, which
475 benefitted from high edge density to spillover and provide services in crops (ground- and to a
476 lesser extent flight-dispersing enemies overwintering outside crops for pest control; non-
477 agricultural specialists for pollination). Due to positive impacts on services and many service
478 providers and negative impacts on pests, edge density thus appeared a more consistent driver
479 for functional biodiversity and service provision than the presence of semi-natural habitat
480 alone (Concepción *et al.* 2012). High diversity of arthropod service providers in such
481 landscapes, confirmed by a positive correlation between abundance and species richness, may

482 further imply functional redundancy. As a result, services supported by these landscapes may
483 be more resilient to environmental change (Oliver *et al.* 2015, Martin *et al.* in press).

484 Landscapes with high edge density did not have lower yields/area than coarse-grained
485 landscapes, in a large portion of composition gradients with varying % SNH and arable land.
486 Though only available from a subset of the data (Table S6), this result indicates that high edge
487 density and its benefits can be combined with maintaining crop yields, within the range of
488 edge density observed here. Accordingly, productive landscapes with edge density between
489 0.2 and 0.4 km/ha may be ideally suited to implement ecological intensification. Cascading
490 (positive) effects on yields of higher service provision and less pests in landscapes with high
491 edge density were not, however, apparent from the available data. Reduced pollination and
492 pest control at low edge density may have been compensated by external inputs in productive
493 landscapes. In addition, other factors combine to impact yields (Gagic *et al.* 2017) and may
494 mask the impact of biodiversity-driven services in the absence of careful standardization
495 (Pywell *et al.* 2015). Intermediate to low yields in landscapes with high % arable, low % SNH
496 and low edge density may underpin the risks of ongoing conventional intensification resulting
497 in yield stagnation or reduction despite high agricultural inputs (Ray *et al.* 2012).

498 Non-linear and interacting effects of landscape predictors denote the importance of variation
499 in the ranges occupied by European landscape gradients between studies. In combination with
500 trait-based response syndromes, these results explain several inconsistencies highlighted in
501 previous work (Kennedy *et al.* 2013; Veres *et al.* 2013; Díaz & Concepción 2016; Holzschuh
502 *et al.* 2016; Rader *et al.* 2016; Tschardtke *et al.* 2016; Karp *et al.* 2018). By covering a wide
503 range of landscapes and responses, this study helps resolve why responses to landscape
504 configuration and composition of arthropod functional groups differ along landscape
505 gradients. In particular, we show that landscape effects and the potential effectiveness of
506 landscape management measures vary according to the ranges of landscape variables captured

507 in each study region, in agreement with theory underlying non-linear responses of organisms
508 to landscape gradients (Concepción *et al.* 2012). Increasing edge density was most effective
509 for arthropods in landscapes with low (<5%) or high (>20%) % SNH. In landscapes with
510 intermediate % SNH, small increases in SNH may dilute populations, evening out the benefits
511 of many edges, before reaching sufficient levels to contribute positively to spillover into
512 fields. In these landscapes, extensive practices such as low-input farming may be the most
513 effective way to enhance arthropod diversity and services in crops (Jonsson *et al.* 2015).
514 Contrary to our hypotheses (Fig. 1), few effects were hump-shaped within the range of tested
515 gradients, thus maxima may not be reached within the measured European gradients.

516 We applied a trait-based framework for agroecosystem communities using response traits that
517 have not been considered in previous work on pollinators (Williams *et al.* 2010; De Palma *et*
518 *al.* 2015; Carrié *et al.* 2017) or grassland arthropods (Gámez-Virués *et al.* 2015), but were
519 important determinants of species' responses to landscape structure. We found that syndromes
520 combining several response traits effectively disentangled pollinator, pest and enemy
521 responses compared to single-trait approaches. Considering such traits with strong
522 mechanistic underpinnings (Bartomeus *et al.* 2018) will increase our ability to derive
523 predictions of the effects of environmental change on communities. Clarification is needed,
524 however, on which trait syndromes correlate with strong impacts on service provision in
525 crops. For instance, non-bees may complement bees for provision of pollination services
526 (Rader *et al.* 2016), but the separate contribution of non-bee pollinators in intensive
527 landscapes is unknown, and according to our results, may be considerably lower. In addition,
528 relative contributions to pest control of natural enemies with different landscape responses,
529 and the importance of high enemy diversity for pest control in real-world landscapes, have yet
530 to be elucidated.

531 *Conclusion*

532 In this synthesis across Europe, we show that within European gradients, a high edge density
533 is beneficial for a wide range of arthropods and the services they provide, and can be
534 combined with high yields in productive landscapes with over 50% arable land. In addition to
535 managing semi-natural habitat amounts, increasing the edge density of these landscapes is a
536 promising pathway to combine the maintenance of arthropod biodiversity and services with
537 continued and sustainable agricultural production. While the strength of these effects for
538 arthropods depends on habitat amount, fine-grained landscapes provided benefits such as less
539 pests and more pollination, which were largely independent of their composition. We further
540 demonstrate a high response diversity of arthropod service providers leading to differing
541 impacts of landscape change within groups of natural enemies, pests and pollinators. We thus
542 call for consideration of mechanism-relevant response traits to catalyze modelling and
543 prediction of the consequences of land-use change on arthropods and ecosystem services in
544 crops.

545

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772 Table 1. Functional response traits included in cluster analyses. Details on classification of
 773 traits for all organisms are provided in Appendix S1, Table S2. The full database of traits for
 774 all species is published at doi:10.5061/dryad.6tj407n.

Trait name	Trait level	Abbreviation	Description
Diet breadth	specialist	(specialist)	Diet restricted to no more than two families of host plants or prey*
	generalist	(generalist)	Generalist diet including a broad range of families
Agricultural specialism	yes	(agsp)	Diet specialists for which hosts or prey are agricultural (crops or pests)
	no	(non agsp)	Diet generalists or diet specialists for which hosts or prey are not agricultural
Diet life history	same diet	(same diet)	Organisms have a similar diet across their life cycle
	different diet	(diff. diet)	Organisms switch diets between life stages (e.g. carnivore larva to nectarivore adult)
Overwintering habitat	crop	(crop)	Organisms may overwinter in or outside crops
	non crop	(non crop)	Organisms overwinter mainly outside crops
Dispersal	ground	(gd)	Dispersal by moving on the ground (wingless or undeveloped wings)
	flight	(flight)	Dispersal by active flight (organisms with developed wings)

	flight / wind	(fl/wind)	Active flyers known to disperse on wind currents
	wind	(wind)	Dispersal by wind or electrostatic currents (ballooning spiders)
Stratum	ground / vegetation	(ground/veg)	Forages by walking or web-building on the ground or in vegetation
	aerial	(aerial)	Forages by flying between target hosts

775 * Diet restricted to one larval ‘microhabitat’ for hoverflies; see Appendix S1.

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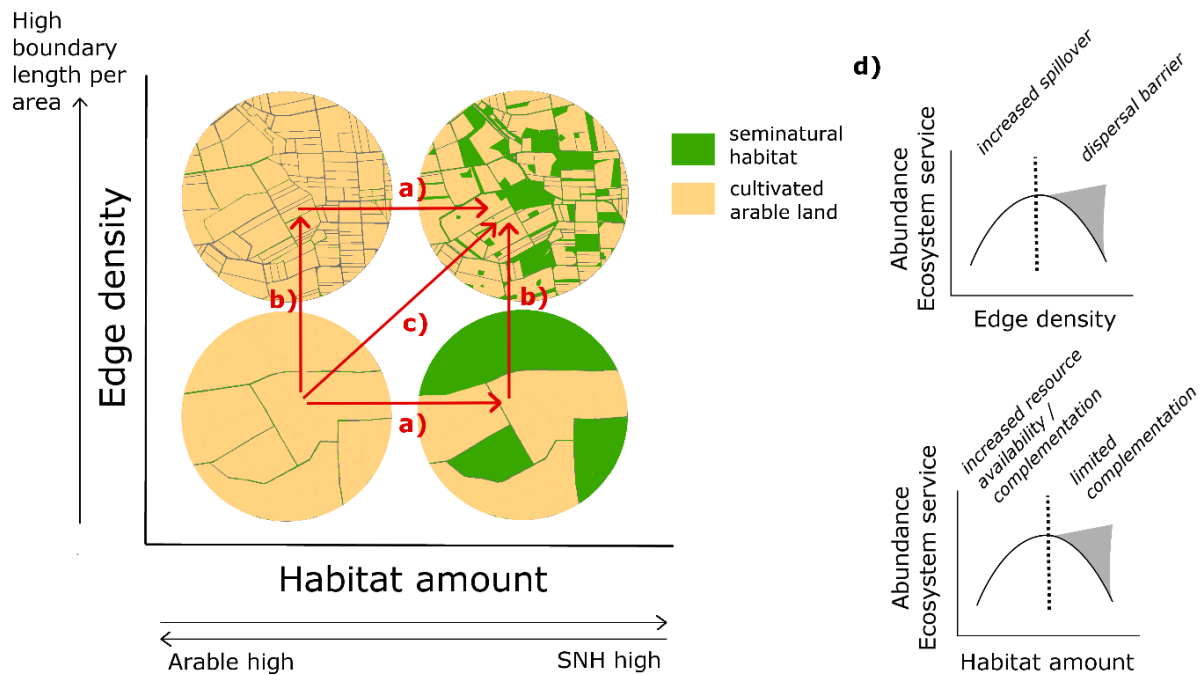
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785 Fig. 1. Conceptual representation of the distinction between landscape composition and
 786 configuration and their possible effects. Four theoretical farming landscapes are viewed from
 787 above (left panel). **a) Landscape composition (increasing habitat amount):** an increase in
 788 the proportion of seminatural habitat (SNH) is reflected, in the absence of forest, by a
 789 decrease in the proportion of cultivated area as arable land is taken out of production. **b)**
 790 **Landscape configuration (increasing edge density):** for the same total amount of crop and
 791 non-crop habitat, decreasing patch sizes and complex shapes lead to an increase in the length
 792 per area of edges (ecotones) among crop fields and between crop and non-crop habitat. **c)**
 793 **Simultaneous increase vs. interactions:** habitat amount and landscape edge density may
 794 increase simultaneously, making it difficult to disentangle the contribution of each to
 795 biodiversity and ecosystem services. However, these variables are not intrinsically correlated.
 796 In addition, interactions may take place that lead to different effects of edge density according
 797 to the relative proportion of crop and non-crop habitats in a landscape. **d) Non-linear effects:**
 798 we hypothesize that effects of landscape composition and configuration on abundance and
 799 services are unimodal, with different mechanisms operating at each end of the gradients. For

800 instance, low resource complementarity due to high amounts of semi-natural habitat, but little
801 cropland may decrease arthropod abundance and/or ecosystem services if organisms benefit
802 from both resource types (e.g. pollinators that benefit from flowering crops or enemies that
803 feed on pest prey, but require resources from semi-natural habitats for reproduction).
804 However, the shape of curve tail ends (grey area) should depend on the state of other
805 variables. For instance, constraints on resource complementation when habitat amount is high
806 should be lifted when edge density increases, facilitating spillover.

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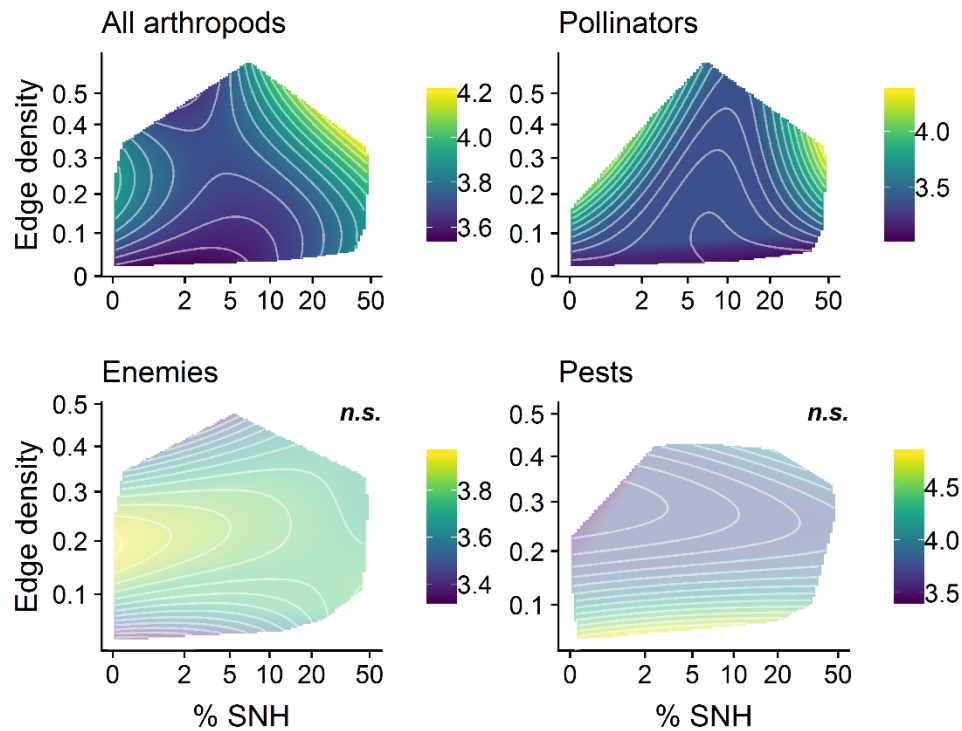
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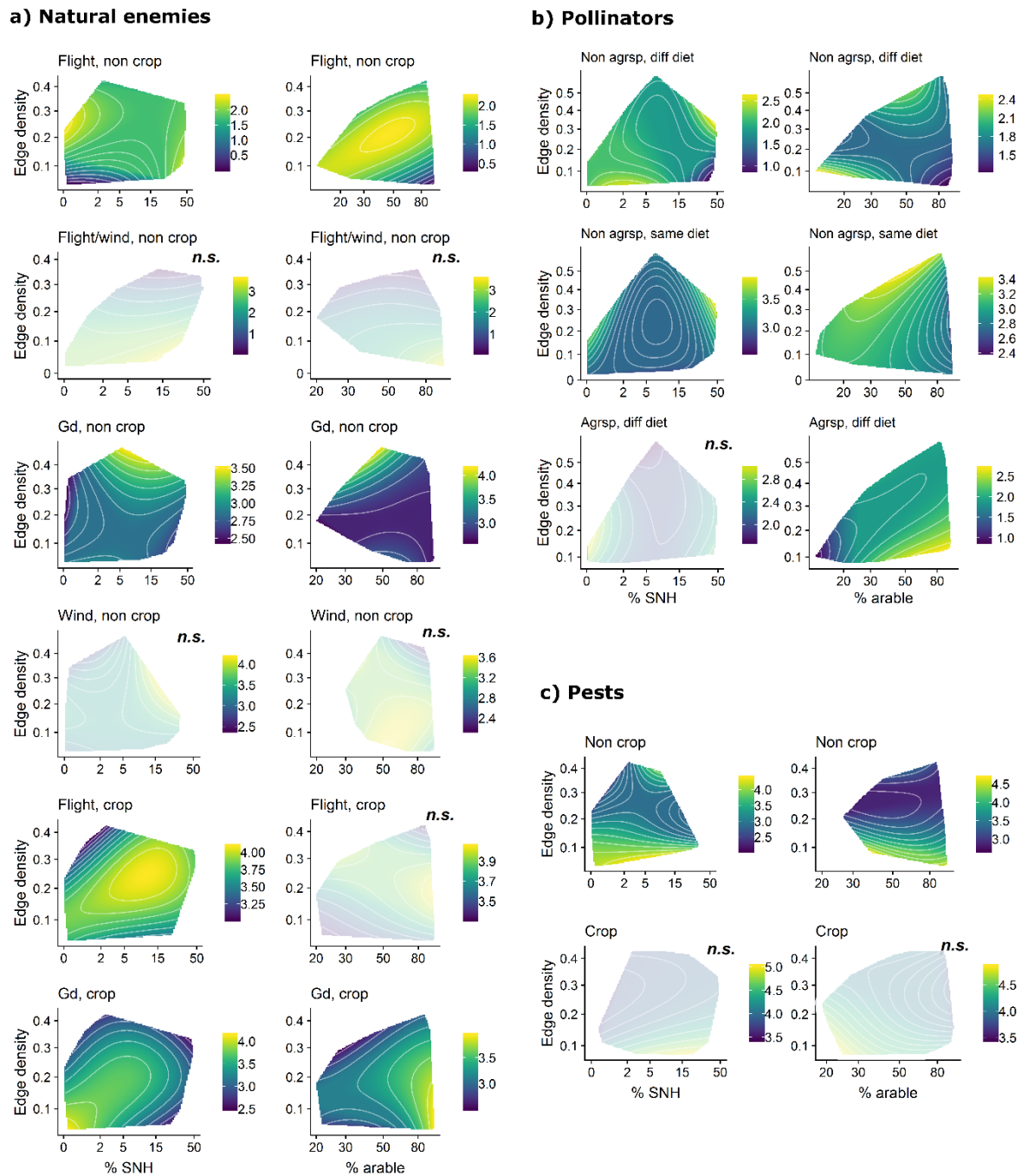
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815 Fig. 2. Heatmaps of the effects of seminatural habitat amount (SNH; composition variable)
 816 and landscape edge density (ED in km/ha; configuration variable) on the abundance of
 817 arthropods (top left) and on functional groups of pollinators, natural enemies, and pests. The
 818 heatmaps can be read like a topographic map, with yellow peaks and blue valleys, and steeper
 819 slopes where line density is high. Yellow indicates areas of highest abundance, blue areas of
 820 lowest abundance (see $\ln(x+1)$ -transformed abundance scale at the right of each panel).
 821 Estimates and 95% confidence intervals (CI) of effects are shown for all radii in Fig. S4.
 822 Results at 1 km radius are shown here. Results are not interpreted (marked 'n.s.' and faded) if
 823 significant effects were obtained at less than two out of six tested radii. Only the area
 824 covering the range of both variables for each response is plotted. Note a log-scale of predictor
 825 variables.



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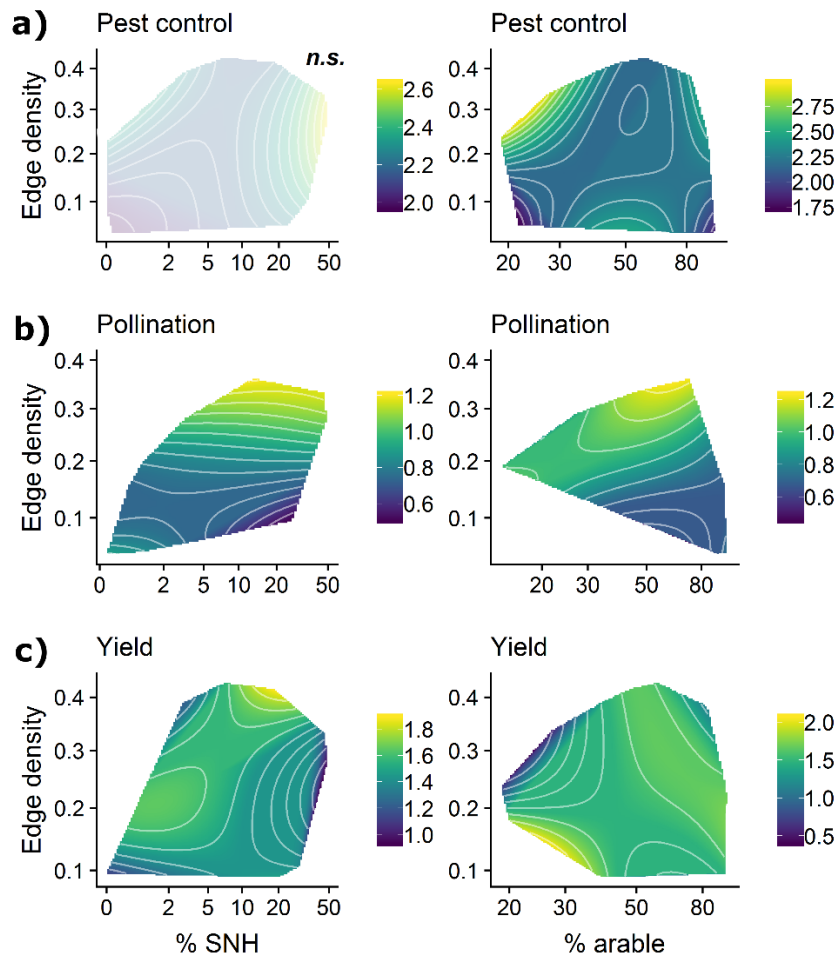
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Fig. 3. Heatmaps of the effects of landscape composition (% SNH, left columns; % arable land, right columns) and landscape configuration (edge density in km/ha) on the abundance of functional response groups of a) natural enemies, b) pollinators, and c) pests. Functional groups were separated into trait syndromes based on cluster regression of six categorical traits (see abbreviations in Table 1; Figs. S2-3). Estimates and 95% CI are shown at all radii in Fig. S5; results are shown here at the 1 km radius. See further graph details in the legend of Fig. 2.

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835 Fig. 4. Heatmaps of the effects of landscape composition (% SNH, left columns; % arable
 836 land, right columns) and landscape configuration (edge density in km/ha) on a) pest control,
 837 b) pollination and c) crop yield in weight per unit area. Response variables represent an
 838 ecosystem service index accounting for differences in methods within and between studies
 839 (see Appendix S1). See Table S3 for detailed units and measurements per study. Blue: lowest
 840 service provision; yellow: highest service provision. Estimates and 95% CI are shown at all
 841 radii in Fig. S6; results are shown here at the 1 km radius. See further graph details in the
 842 legend of Fig. 2.