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The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agro-ecosystem services across Europe

Emily A. Martin[1*], Matteo Dainese[2], Yann Clough[3], András Báldi[4], Riccardo Bommarco[5], Vesna Gagic[6], Michael Garratt[7], Andrea Holzschuh[1], David Kleijn[8], Anikó Kovács-Hostyánszki[4], Lorenzo Marini[9], Simon G. Potts[7], Henrik Smith[3], Diab Al Hassan[10], Matthias Albrecht[11], Georg K.S. Andersson[3], Josep D. Asís[12], Stéphanie Aviron[13], Mario Balzan[14], Laura Baños-Picón[12], Ignasi Bartomeus[15], Péter Batáry[16], Francoise Burel[10], Berta Caballero-López[17], Elena D. Concepción[18], Valérie Coudrain[19], Juliana Dänhardt[3], Mario Diaz[18], Tim Diekötter[20], Carsten F. Dormann[21], Rémi Duflot[22], Martin H. Entling[23], Nina Farwig[24], Christina Fischer[25], Thomas Frank[26], Lucas A. Garibaldi[27], John Hermann[20], Felix Herzog[11], Diego Inclán[28], Katja Jacot[11], Frank Jauker[29], Philippe Jeanneret[11], Marina Kaiser[30], Jochen Krauss[1], Violette Le Féon[31], Jon Marshall[32], Anna-Camilla Moonen[33], Gerardo Moreno[34], Verena Riedinger[1], Maj Rundlöf[35], Adrien Rusch[36], Jeroen Scheper[37], Gudrun Schneider[1], Christof Schüepp[38], Sonja Stutz[39], Louis Sutter[11], Giovanni Tamburini[5], Carsten Thies[40], José Tormos[12], Teja Tscharntke[41], Matthias Tschumi[11], Deniz Uzman[42], Christian Wagner[43], Muhammad Zubair-Anjum[44], Ingolf Steffan-Dewenter[1]

[1] Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg, Germany

[2] Institute for Alpine Environment, EURAC Research, Viale Druso 1, 39100 Bolzano, Italy

[3] Centre for Environmental and Climate Research, Lund University, 22362, Lund, Sweden

[4] MTA Centre for Ecological Research, Institute for Ecology and Botany, Lendület Ecosystem Services Research Group, Alkotmány u. 2-4, 2163 Vácrátót, Hungary

[5] Department of Ecology, Swedish University of Agricultural Sciences, SE-750 07 Uppsala, Sweden

[6] Commonwealth Scientific and Industrial Research Organisation, Dutton Park, Queensland, Australia

[7] Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, Reading University, RG6 6AR, UK

[8] Plant Ecology and Nature Conservation Group, Wageningen University, Droevendaalsesteeg 3, 6708PB Wageningen, The Netherlands

[9] DAFNAE, University of Padova, Viale dell'Università 16, 35020 Legnaro (Padova), Italy
[10] UMR 6553 Ecobio, CNRS, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes Cedex, France
[11] Agroecology and Environment, Agroscope, Reckenholzstrasse 191, 8046 Zurich, Switzerland
[12] Departamento de Biología Animal (Área de Zoología), Facultad de Biología, Universidad de Salamanca, Campus Miguel de Unamuno s/n, 37007 Salamanca, Spain
[13] UMR BAGAP - INRA, Agrocampus Ouest, ESA, 49000 Angers, France
[14] Institute of Applied Sciences, Malta College of Arts, Science and Technology (MCAST), Paola, Malta
[15] Estación Biológica de Doñana (EBD-CSIC). E-41092 Sevilla, Spain
[16] MTA ÖK Lendület Landscape and Conservation Ecology Research Group, Alkotmány u. 2-4, 2163 Vácrátót, Hungary
[17] Department of Arthropods, Natural Sciences Museum of Barcelona, Castell dels Tres Dragons, Picasso Av, 08003 Barcelona, Spain
[18] Department of Biogeography and Global Change, National Museum of Natural Sciences, Spanish National Research Council (BGC-MNCN-CSIC), C/ Serrano 115 bis, E-28006 Madrid, Spain
[19] Mediterranean Institute of Marine and Terrestrial Biodiversity and Ecology (IMBE), Aix-Marseille University, CNRS, IRD, Univ. Avignon, 13545 Aix-en-Provence, France
[20] Department of Landscape Ecology, Kiel University, Olshausenstrasse 75, 24118 Kiel, Germany
[21] Biometry & Environmental System Analysis, University of Freiburg, Germany
[22] Department of Biological and Environmental Sciences, University of Jyväskylä, Finland
[23] Institute for Environmental Sciences, University of Koblenz-Landau, Fortstr. 7, 76829 Landau, Germany
[24] Department of Conservation Ecology, Faculty of Biology, Philipps-University Marburg, Karl-von-Frisch Str. 8, 35043 Marburg, Germany
[25] Restoration Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, 85354 Freising, Germany
[26] University of Natural Resources and Life Sciences, Department of Integrative Biology and Biodiversity Research, Institute of Zoology, Gregor Mendel Straße 33, A-1180 Vienna, Austria

[27] Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural (IRNAD), Sede Andina, Universidad Nacional de Río Negro (UNRN) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mitre 630, CP 8400, San Carlos de Bariloche, Río Negro, Argentina
[28] Instituto Nacional de Biodiversidad, INABIO – Facultad de Ciencias Agícolas, Universidad Central del Ecuador, Quito 170129, Ecuador
[29] Department of Animal Ecology, Justus Liebig University, Heinrich-Buff-Ring 26-32, D-35392 Giessen, Germany
[30] Faculty of Biology, Institute of Zoology, University of Belgrade, Studentski trg 16, Belgrade 11 000, Serbia
[31] INRA, UR 406 Abeilles et Environnement, Site Agroparc, 84914 Avignon, France
[32] Marshall Agroecology Ltd, Winscombe, UK
[33] Institute of Life Sciences, Scuola Superiore Sant'Anna, Piazza Martiri della Libertà 33, I-56127 Pisa, Italy
[34] INDEHESA, Forestry School, Universidad de Extremadura, Plasencia 10600, Spain
[35] Department of Biology, Lund University, 223 62 Lund, Sweden
[36] INRA, UMR 1065 SAVE, ISVV, Université de Bordeaux, Bordeaux Sciences Agro, F-33883 Villenave d'Ornon, France
[37] Animal Ecology Team, Wageningen Environmental Research, Droevendaalsesteeg 3, 6708 PB Wageningen, The Netherlands
[38] Institute of Ecology and Evolution, University of Bern, CH-3012 Bern, Switzerland
[39] CABI, Rue des Grillons 1, 2800 Delémont, Switzerland
[40] Natural Resources Research Laboratory, Bremer Str. 15, 29308 Winsen, Germany
[41] Agroecology, University of Göttingen, Grisebachstrasse 6, 37077 Göttingen, Germany
[42] Department of Crop Protection, Geisenheim University, Von-Lade-Str. 1, 65366 Geisenheim, Germany
[43] LfL, Bayerische Landesanstalt für Landwirtschaft, Institut für Ökologischen Landbau, Bodenkultur und Ressourcenschutz, Lange Point 12, 85354 Freising, Germany
[44] Department of Zoology & Biology, Faculty of Sciences, Pir Mehr Ali Shah Arid Agriculture University Rawalpindi, Pakistan

[*] Corresponding author: email: emily.martin@uni-wuerzburg.de, phone: +499313183876.

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Abstract

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

INTRODUCTION

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

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

The configuration of landscapes (size, shape and spatial arrangement of land-use patches), in addition to their composition (proportion of land-use types), is increasingly suggested as a key factor in determining biodiversity and associated ecosystem services in agricultural landscapes (Fahrig 2013). However, studies have only begun to disentangle the relative roles of the composition *vs*. the configuration of habitats and fields within landscapes (Fig. 1; Fahrig 2013; Haddad *et al.* 2017). Landscape configuration can be measured as the density of edges between crop fields and their surroundings, including neighboring crops and non-crop areas. Complex landscapes where small and/or irregularly shaped fields and habitat patches prevail have a high density of edges. Due to increased opportunities for exchange, these landscapes are likely to support spillover of dispersal-limited populations between patches (Smith *et al.* 2014; Fahrig 2017). This may enhance populations' survival in the face of disturbance and their potential to provide services in crops (Boetzl *et al.* 2019). Further, if landscapes with high edge density are also spatially and temporally diverse in their composition, organisms in these landscapes may benefit from landscape-scale resource complementation and supplementation (Dunning *et al.* 1992). In this context, areas offering refuges or complementary food resources may encompass uncropped (semi-natural) areas, but also neighboring crops with asynchronous phenology, different host species and/or variable timing and intensity of management interventions (Vasseur *et al.* 2013; Schellhorn *et al.* 2015). However, previous studies have found contrasting effects of increasing configurational complexity for different taxa (Concepción *et al.* 2012; Plećaš *et al.* 2014; Duflot *et al.* 2015; Fahrig *et al.* 2015; Gámez-Virués *et al.* 2015; Perović *et al.* 2015; Martin *et al.* 2016; Bosem Baillod *et al.* 2017; Hass *et al.* 2018). Thus, there is currently no consensus on the importance of landscape configuration for arthropods and the services they provide in crops (Seppelt *et al.* 2016; Perović *et al.* 2018). Further, interactions between landscape composition and configuration might explain seemingly contradictory results, but have rarely been tested in part due to a lack of independent landscape gradients (but see Coudrain *et al.* 2014; Bosem Baillod *et al.* 2017).

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

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

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

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

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

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

MATERIAL AND METHODS

Data collection and collation

Data holders were approached through networks of researchers with the aim of collecting raw data from a representative sample of studies performed in European crops. After initial collection, data were screened for missing countries or crops systems, and requests were targeted at researchers having published in these areas. Of 77 proposed studies, 58 provided data with sufficient site replication and high resolution land-use maps (Table S1, Appendices S1, S2 in Supporting Information). Requested data were arthropod abundance per unit area and time (species richness when available) and measures of pollination, pest control and yields, sampled along gradients of landscape composition and configuration in ≥8 sites. Sites included annual and perennial crop fields, managed grasslands, field margins and orchards. Farms were conventional, low-input conventional or organic. Data were collated and standardized as described in Appendix S1. After preliminary analyses, we excluded organic sites because few studies compared conventional and organic farms in similar landscapes. This led to a total of 49 studies and 1,637 site replicates from 1,515 distinct landscapes (circular map sectors; Appendix S1, Fig. S1), some sites having been sampled in multiple studies.

Landscape variables

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

Similarly, several measures of landscape configuration exist. Among them, the density of edges available for exchange between landscape patches theoretically underpins mechanisms of spillover and resource complementarity for biodiversity and services (see Introduction), and has been frequently used in other studies (e.g. Holzschuh et al. 2010; Concepción et al. 2012). We thus measured landscape configuration as the total length of edges per area of each landscape sector (edge density ED, in km/ha) between crop fields and their surroundings. Hereby, we consider the combined effects of crop / crop (between fields) and crop / non-crop edges (Fig. 1). Both interfaces may enhance arthropod movements in and out of fields (Schellhorn *et al.* 2015). At radii up to 0.5 km, ED is negatively related to mean field size and positively to the density of edges per area of arable land (Fig. S2). Importantly, ED reflects the grain of whole landscapes including non-crop elements and crops. Thus landscapes with high ED have comparatively small fields and non-crop patches. A decrease in ED is related to an increase in size of both field and/or non-crop patches, and reflects a lower total density of edges available for exchange in the whole landscape.

Functional groups and arthropod traits

We classified above-ground arthropods into functional groups of pollinators, pests and natural enemies of pests (Appendix S1, Table S2). Organisms that are predators or herbivores as larvae, but pollinators as adults were classified according to the life stage sampled. Arthropods that could not be classified into these groups (Appendix S1) were included in analyses of total arthropod abundance, as they contribute to overall farmland biodiversity, but not in separate analyses of pollinators, pests and natural enemies (see Statistical analyses).

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

Statistical analyses

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

To account for collinearity of composition variables (Fig. S2), we performed two sets of models including either % SNH or % arable. Correlations between edge density and composition variables were low within and across studies (Fig. S2; mean within-study Spearman rho 0.05, SD 0.2, mean variance inflation factor of models with all arthropods 2.7, SD 1.8), but some studies showed high correlation in specific years and scales (Table S4). We thus ran analyses including and excluding these studies. As no differences were found in overall results, we present analyses including all studies (Appendix S1).

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

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

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

RESULTS

Abundance of arthropods and functional groups

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

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

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

Trait syndromes of enemies, pollinators and pests

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

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

Pests able to overwinter in crops showed few effects of landscape variables across scales. But pests considered to leave crops over winter were six times less abundant in landscapes with high edge density (0.2-0.4 km/ha), regardless of their composition (Fig 3c, S6). Due to an increase beyond this range at intermediate % SNH, 0.2-0.4 km/ha of edges represented an area of minimum pest density along the observed gradients.

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

Pest control, pollination and yields

Pest control, pollination and yields are given for a subset of studies (Tables S3, S6; Figs. 4, S7). Pest control by natural enemies was highest in landscapes with low % arable land (<40%) and high edge density, where it increased 1.4-fold compared to landscapes with low edge density. It was lowest in coarse-grained landscapes (low edge density) with either low or high % arable land (Fig. 4a). Pollination increased with edge density: it was 1.7 times higher in fine-grained compared to coarse-grained landscapes regardless of % SNH or % arable land. Low pollination was observed in landscapes with >70% arable land and at edge densities <0.1 km/ha (Fig. 4b right panel). Yields showed a variable pattern (Fig. 4c, S7). They were highest in landscapes with 10-20% SNH at high edge density (Fig. 4c left panel). Lowest yields were achieved in landscapes with <40% arable land and high edge density (Fig. 4c right panel). In a range of landscapes including a large range of edge density and % arable land, intermediate to high yields were maintained. The variance explained by landscape predictors in models of pest control, pollination and yields averaged 0.14, SD 0.08 (mean maximal R^2m across scales; mean maximal R^2c 0.60, SD 0. 09).

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

DISCUSSION

This synthesis shows that the response of arthropod abundance and services to landscape predictors is non-linear across Europe and depends on interactions between landscape composition and configuration, and on the response traits of arthropods. Overall, arthropods were most abundant in landscapes that combine high edge density with high proportions of semi-natural habitat. Functional groups of pollinators, enemies and pests did not strongly reflect this pattern. Rather, trait syndromes within groups showed contrasting trends. Pollinators that do not feed on pests or crops as larvae (non-pest butterflies, non-aphidophagous syrphids, bees), and flying and ground-dwelling enemies considered to overwinter mainly outside crops, benefited from high edge density at low or high habitat amount and may require a high density of ecotones as exchange interfaces in order to spillover between and into crops (Concepción *et al.* 2012; Tscharntke *et al.* 2012; Hass *et al.* 2018). For organisms with limited dispersal ability, this requirement is likely due to the need to recolonize crops in spring. However, the same driver affected strong aerial dispersers such as wasps and butterflies, for which it may be more related to a high sensitivity to disturbance within fields, and/or to the need for resource complementation through a high diversity of available plants and prey (Sutter *et al.* 2017) or nesting sites. Such diverse resources can be found in neighboring semi-natural habitats (e.g. nest sites; Holland *et al.* 2016), but also in adjoining crops (pollen and nectar from crops and weeds, host plants or prey for herbivores and predators). Indeed, a high number of separate field units is the first requirement to support a high diversity of arable crops at organism-relevant scales. Landscapes with high vs. low edge density may also differ in their crop composition and/or diversity, with associated impacts on the arthropod community.

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

Pests overwintering outside crops were least abundant, and pollination and pest control were highest, in landscapes with high edge density, particularly within the range of 0.2-0.4 km/ha. In agreement with Rusch *et al.* (2016), pest control was also highest at low % arable land. But for pests and pollination, edge density effects occurred largely independently of landscape composition. Based on trait syndrome patterns, pest control and pollination appear to have been largely driven by organisms without strong links to agricultural resources, which benefitted from high edge density to spillover and provide services in crops (ground- and to a lesser extent flight-dispersing enemies overwintering outside crops for pest control; non-agricultural specialists for pollination). Due to positive impacts on services and many service providers and negative impacts on pests, edge density thus appeared a more consistent driver for functional biodiversity and service provision than the presence of semi-natural habitat alone (Concepción *et al.* 2012). High diversity of arthropod service providers in such landscapes, confirmed by a positive correlation between abundance and species richness, may further imply functional redundancy. As a result, services supported by these landscapes may be more resilient to environmental change (Oliver *et al.* 2015, Martin *et al*. in press).

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

Non-linear and interacting effects of landscape predictors denote the importance of variation in the ranges occupied by European landscape gradients between studies. In combination with trait-based response syndromes, these results explain several inconsistencies highlighted in previous work (Kennedy *et al.* 2013; Veres *et al.* 2013; Díaz & Concepción 2016; Holzschuh *et al.* 2016; Rader *et al.* 2016; Tscharntke *et al.* 2016; Karp *et al.* 2018). By covering a wide range of landscapes and responses, this study helps resolve why responses to landscape configuration and composition of arthropod functional groups differ along landscape gradients. In particular, we show that landscape effects and the potential effectiveness of landscape management measures vary according to the ranges of landscape variables captured in each study region, in agreement with theory underlying non-linear responses of organisms to landscape gradients (Concepción *et al.* 2012). Increasing edge density was most effective for arthropods in landscapes with low (<5%) or high (>20%) % SNH. In landscapes with intermediate % SNH, small increases in SNH may dilute populations, evening out the benefits of many edges, before reaching sufficient levels to contribute positively to spillover into fields. In these landscapes, extensive practices such as low-input farming may be the most effective way to enhance arthropod diversity and services in crops (Jonsson *et al.* 2015). Contrary to our hypotheses (Fig. 1), few effects were hump-shaped within the range of tested gradients, thus maxima may not be reached within the measured European gradients.

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

Conclusion

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

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SUPPORTING INFORMATION

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Table 1. Functional response traits included in cluster analyses. Details on classification of traits for all organisms are provided in Appendix S1, Table S2. The full database of traits for 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

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

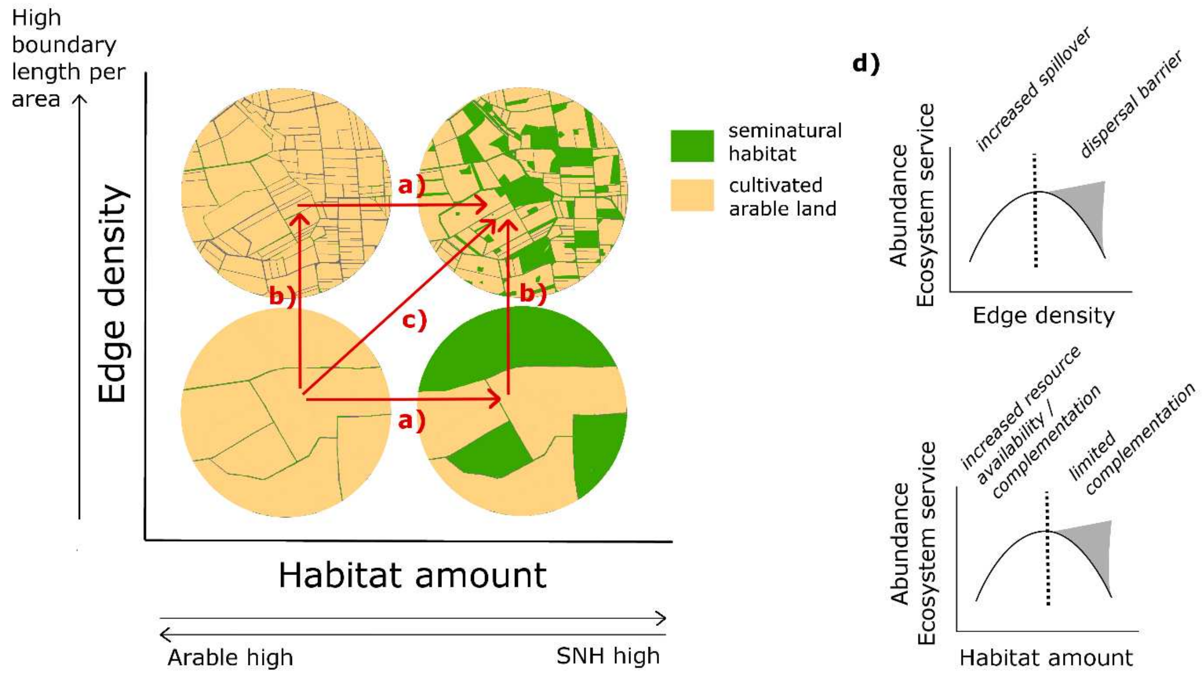

Fig. 1. Conceptual representation of the distinction between landscape composition and configuration and their possible effects. Four theoretical farming landscapes are viewed from above (left panel). **a) Landscape composition (increasing habitat amount):** an increase in the proportion of seminatural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

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

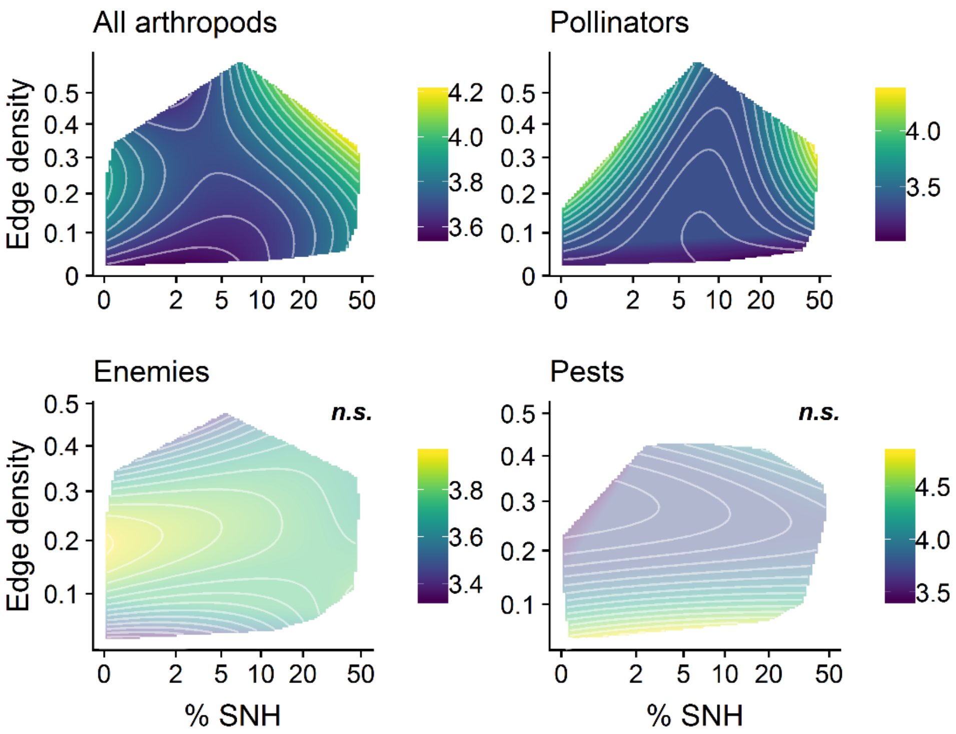

Fig. 2. Heatmaps of the effects of seminatural habitat amount (SNH; composition variable) and landscape edge density (ED in km/ha; configuration variable) on the abundance of arthropods (top left) and on functional groups of pollinators, natural enemies, and pests. The heatmaps can be read like a topographic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

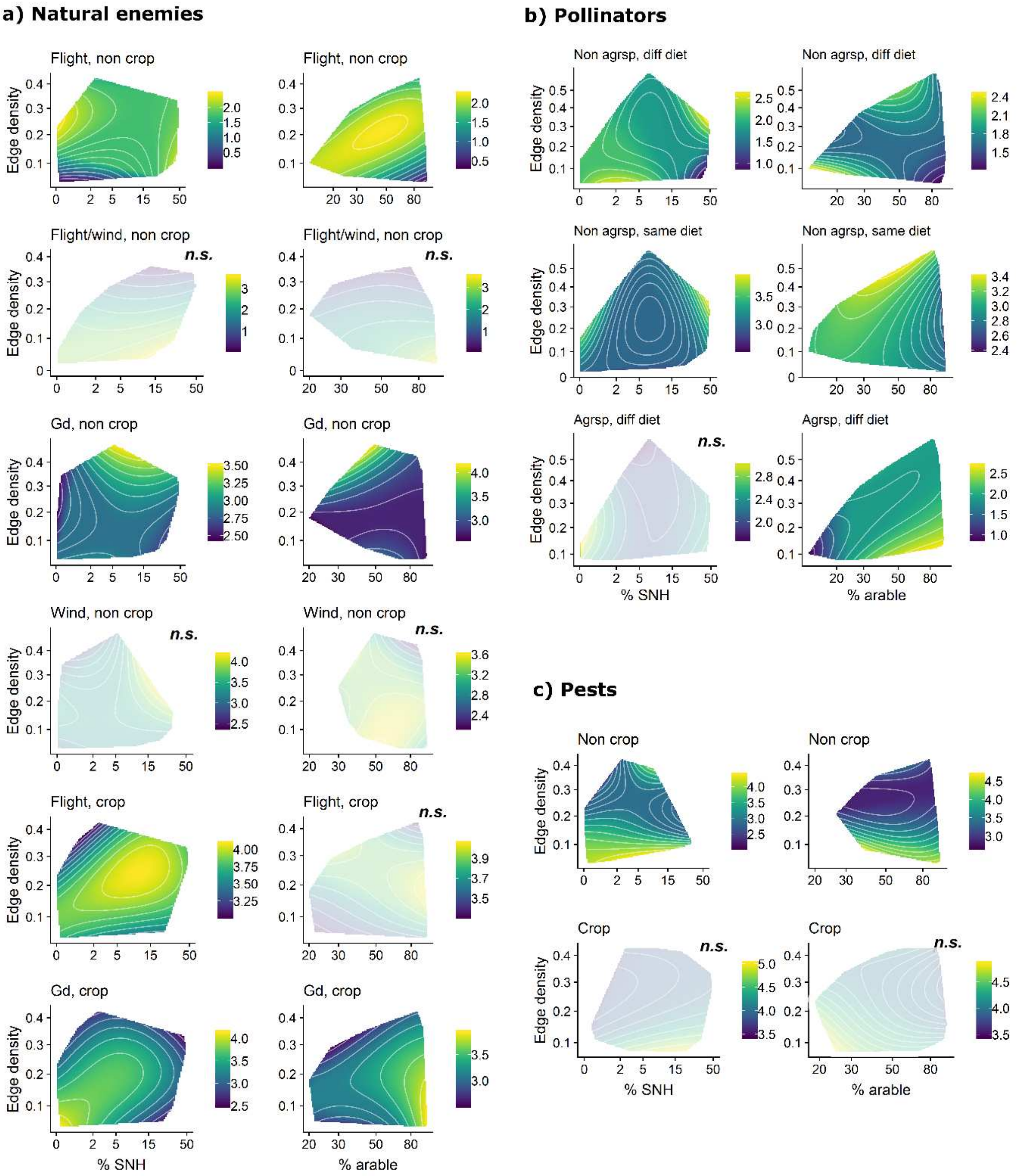

Fig. 3. Heatmaps of the effects of landscape composition (% SNH, left columns; % arable land, right columns) and landscape configuration (edge density in km/ha) on the abundance of functional response groups of a) natural enemies, b) pollinators, and c) pests. Functional groups were separated into trait 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.

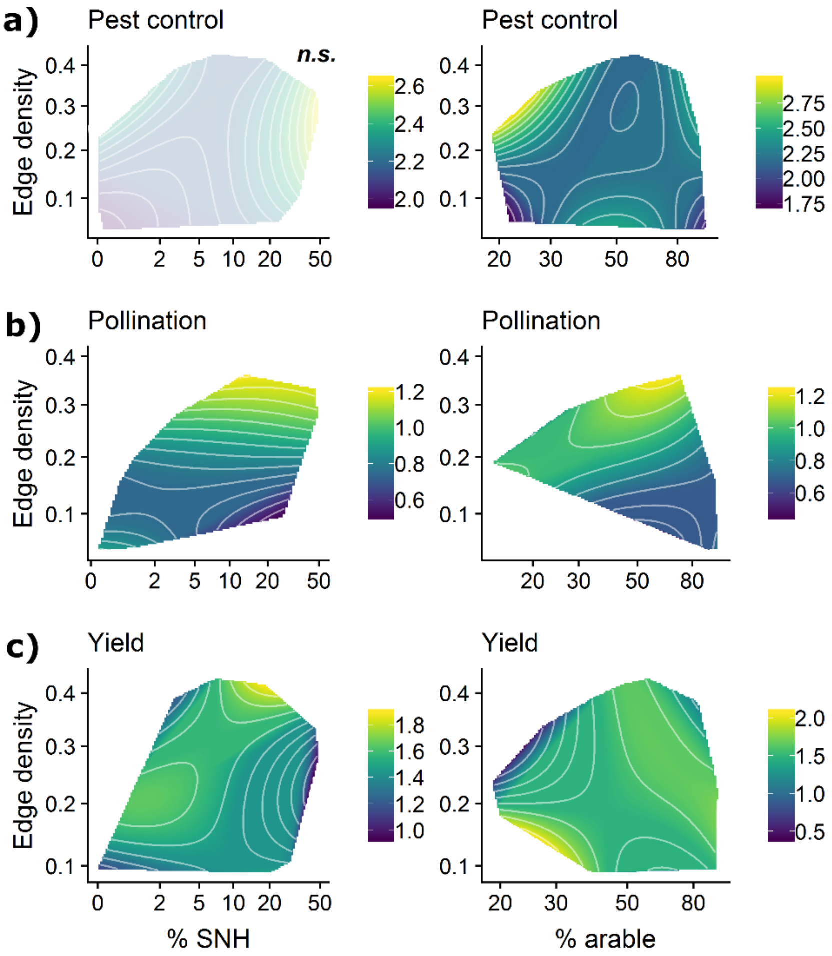

Fig. 4. Heatmaps of the effects of landscape composition (% SNH, left columns; % arable land, right columns) and landscape configuration (edge density in km/ha) on a) pest control, b) pollination and c) crop yield in weight per unit area. Response variables represent an ecosystem service index accounting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