

Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity

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Summary

1. Insectivorous birds are increasingly recognized for the crucial pest control services they provide to agroecosystems. While both the foraging activity and functional diversity of birds are enhanced by multiscale habitat heterogeneity, little is known about how these relationships may influence avian top-down control of insects. Specifically, interactive effects of bird community structure and habitat heterogeneity on pest control across spatial scales have rarely been explored.

2. We sampled bird communities and measured avian predation on plasticine model prey, as a proxy for lepidopteran pest control, in 20 vineyards of south-western France. Vineyards differed both in sward heterogeneity at the local scale and amount of surrounding semi-natural habitats at the landscape scale. Functional diversity metrics and community-weighted mean traits were computed for bird communities based on a species–trait table including diet, foraging method, nesting site, migration strategy, laying date, home range size, clutch size and body mass. We used mixed models to test for the interacting effects of habitat heterogeneity and bird functional diversity on avian predation rates of plasticine prey.

3. Contrary to expectations, bird functional diversity decreased with landscape-scale heterogeneity, but was higher in vineyards managed with heterogeneous sward structures. In contrast, foliage-gleaning insectivores were more abundant in landscapes supporting more semi-natural habitats, suggesting an increase in their contribution to pest control along the landscape heterogeneity gradient. Accordingly, we found that avian predation on plasticine prey increased with bird functional evenness both in more heterogeneous vineyards at the local scale and in landscape mosaics supporting more semi-natural habitats.

4. *Synthesis and applications.* Our study demonstrates that habitat heterogeneity at both local and landscape scales influenced avian insectivory in vineyard agroecosystems by interacting with bird community structure. It provides important insights for ecological intensification in vineyards, pointing out that management options need to be adapted to both the functional composition of local bird communities and landscape context. We suggest that both on-field and off-field management can be used to enhance natural pest control services provided by birds in vineyards, especially by favouring sward heterogeneity and patches of semi-natural habitats within large vineyard stands at the landscape scale.

Key-words: agroecosystems, avian predation, bird communities, community-weighted mean traits, ecosystem services, functional insectivory, pest control, plasticine caterpillars, semi-natural habitats, vineyard management

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Introduction

Natural pest control is a major ecosystem service delivered by a wide range of organisms, expected to offer a sustainable solution to pest management in agroecology (Chaplin-Kramer *et al.* 2011; Martin *et al.* 2013; Rusch *et al.* 2016). Recent literature reviews have highlighted the important role of insectivorous birds feeding on pest populations in different agroecosystems (Sekercioglu 2006; Wenny *et al.* 2011; Maas *et al.* 2015). Birds are especially efficient arthropod predators in farmland, where 50% of birds are predominantly feeding on insects, and 75% consume invertebrates at least occasionally (Wenny *et al.* 2011; Whelan, Sekercioglu & Wenny 2015). Avian predation on pest insects has been studied in various natural and agricultural systems, including vineyards, and most studies report a marked reduction in invertebrate biomass by birds, usually ranging from 20% to 70% (Sekercioglu 2006; Barbaro & Battisti 2011; Jedlicka, Letourneau & Cornelisse 2014). This predation not only lowers herbivore abundance but also significantly reduces leaf damage and plant mortality, potentially leading to up to 60% increase in crop yield or fruit production (Mols & Visser 2002; Mäntylä, Klemola & Laaksonen 2011; Whelan, Sekercioglu & Wenny 2015). However, despite an increasing body of evidence demonstrating the importance of birds in providing ecosystem services, the link between the functional composition of bird communities and the magnitude of ecosystem services they provide remains poorly understood (Philpott *et al.* 2009; Cadotte, Carscadden & Mirotnick 2011; Wenny *et al.* 2011).

Extensive studies of the relationships between species richness and ecosystem functions, including herbivore suppression by predators, have generally concluded that higher predator richness is associated with greater arthropod removal (Letourneau *et al.* 2009; Griffin, Byrnes & Cardinale 2013; De la Mora, García-Ballinas & Philpott 2015). However, there is a need for a more mechanistic understanding of the relationships between predation rates and both the species and functional composition of insectivorous bird communities (Philpott *et al.* 2009; Maas *et al.* 2015). As not all species contribute equally to ecosystem functions, it is now largely accepted that taking into account both taxonomic and functional composition of predator communities would provide a deeper understanding of the processes shaping ecosystem functions (Petchey & Gaston 2006; Hillebrand, Bennett & Cadotte 2008; Cadotte, Carscadden & Mirotnick 2011). Predation rates can be affected either by predator species abundance and richness (De la Mora, García-Ballinas & Philpott 2015) or by single- and multitrait functional metrics (Crowder *et al.* 2010; Rusch *et al.* 2015). For example, avian insectivory may be best predicted by bird functional evenness, which measures the equidistribution of trait abundances within bird communities (Barbaro *et al.* 2014), or alternatively, by the abundance of foraging insectivorous birds (Berezki *et al.* 2014). Several studies

have also pointed out the key role played by a small number of species within the bird community, or even by a single species of functional insectivore as the main provider of pest predation in forest and farmland ecosystems (Mäntylä, Klemola & Haukioja 2004; Maas *et al.* 2015; Muiruri, Rainio & Koricheva 2016).

Thus, more work is needed to identify the primary components of bird community structure that drive natural pest control in agroecosystems (Philpott *et al.* 2009; Maas *et al.* 2015). Our understanding of avian predation patterns is also limited by a lack of studies exploring how rates of insectivory vary across spatial scales from plot to ecosystem level (Whelan, Sekercioglu & Wenny 2015). Trophic interactions and natural pest control services in agroecosystems depend on variables acting at multiple spatial scales, including local habitat structure, landscape context and their interactions (Martin *et al.* 2013; De la Mora, García-Ballinas & Philpott 2015; Tamburini *et al.* 2015). This appears particularly true for bird communities, which depend on both local habitat structure, especially sward heterogeneity for farmland birds, and landscape matrix composition (Vickery & Arlettaz 2012; Lindenmayer *et al.* 2015; Pithon *et al.* 2016). However, it is still unclear at which spatial scales environmental drivers act on avian insectivory and how exactly these drivers affect the relationship between bird community structure and predation rates (Martin *et al.* 2013; Barbaro *et al.* 2014; Berezki *et al.* 2014; Muiruri, Rainio & Koricheva 2016).

The hypothesis that landscape context modulates the effects of local management on biodiversity and ecosystem services has been formulated as the 'intermediate landscape complexity hypothesis' (Kleijn *et al.* 2011; Tscharnkte *et al.* 2012). According to this hypothesis, the benefits of local management on biodiversity and associated ecosystem services are lower in more complex, heterogeneous landscapes (i.e. with a high proportion of semi-natural habitats) or in extremely simplified landscapes (i.e. only croplands) than in landscapes of intermediate compositional heterogeneity (Fahrig *et al.* 2011). Actually, 'complex' landscapes already support high levels of biodiversity, while simplified ones only harbour a species-poor regional pool with limited impact on ecosystem services (Tscharnkte *et al.* 2012). To our knowledge, this hypothesis has never been tested using bird communities and the natural pest control service they provide. Therefore, in this study, we examined how habitat heterogeneity modulates the relationship between bird communities and avian insectivory in vineyards, at both local and landscape scales. We hypothesized that: (i) landscape-scale heterogeneity increased bird functional diversity; (ii) landscape heterogeneity interacted with bird functional diversity to enhance avian insectivory in landscapes mixing vineyards and semi-natural habitats; and (iii) landscape heterogeneity modulated the local-scale effect of sward management on predation rates by favouring foliage-gleaning insectivorous birds. In addition, we tested whether single-trait metrics of functional composition (community-weighted mean

traits) perform as well or even better than multitrait indices to predict predation rates (Rusch *et al.* 2015).

Materials and methods

STUDY SITES

The study area was located in Aquitaine, south-western France, a region historically important for wine production currently covering a total of 145 000 ha of vineyards producing ca 7 millions of hL in 2014 (Fig. 1). We selected 20 vineyards along a landscape heterogeneity gradient based on the proportion of semi-natural habitats (SNH), including both woodlands and semi-natural grasslands, in a 500-m-radius buffer around sampled plots. The sampled range of SNH % cover lies between 0 and 68% of the landscape buffer areas, and higher SNH cover was considered to indicate higher surrounding landscape heterogeneity for a given vineyard. Previous analyses of other buffer radii (100, 250, 750 and 1000 m) have shown that 500 m was the scale best correlated with most bird community metrics. Local habitat heterogeneity was defined by the management intensity of inter-row vegetation within vine ranks: (i) homogeneous grass cover within the entire plot (i.e. low local habitat heterogeneity); and (ii) partial (ca. 50%) grass cover due to soil tillage in half of the inter-rows (i.e. high local heterogeneity). Along the landscape heterogeneity gradient, nine vineyards had partial grass cover (i.e. soil tillage in half of the inter-rows) and 11 had full grass cover (i.e. no tillage in the inter-rows).

BIRD COMMUNITIES

Bird communities were sampled using transect counts, where all birds heard and seen were recorded except flyovers, within a

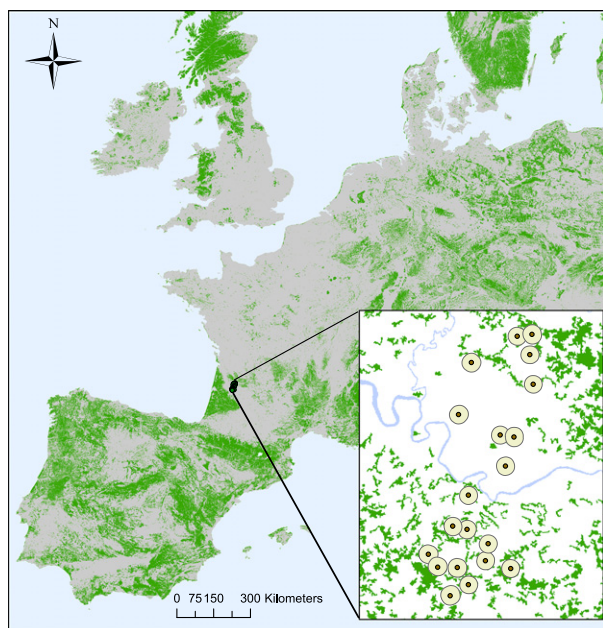


Fig. 1. Location map of sampled vineyards in the Aquitaine region, south-western France (Saint Emilion and Entre-Deux-Mers areas of winegrape production). Points and circles represent the location of the 20 experimental plots and surrounding landscape buffers. Forest cover is indicated in dark green. The study area covers ca 25 × 30 km, that is 75 000 ha.

width of 100 m, that is 50 m from the observer on each transect side (Buckland 2006). We considered that species detectability did not vary among the sampled vineyards due to the highly similar and homogeneous structure of vine ranks. Transects were performed by one trained observer (LB) early in the morning (6:00–10:00 am) only in days without heavy rain or wind. Bird counts were conducted twice in 2013. The first visit was achieved from 18th to 25th of April (early-season breeders) and the second visit from 3rd to 5th of June (late-season breeders). For each species, the highest abundance among the two visits was used as a standardized estimate of abundance per plot for further analyses. Functional insectivore abundance and richness were calculated by cumulating the abundance of species sharing a similar combination of bird traits regarding both diets, foraging techniques and habitat use (Jones, Sieving & Jacobson 2005). A bird species was considered a 'functional insectivore' in vineyards when likely to attack insect prey on vine twigs, that is bird species that were at the same time: (i) insectivorous during the breeding period; (ii) predominantly foraging by foliage gleaning or by hawking; and (iii) using vineyards as breeding and/or foraging habitats.

BIRD INSECTIVITY

Bird insectivory was assessed using plasticine models mimicking lepidopteran pest larvae, a type of prey commonly consumed by insectivorous birds in various ecosystems (Berezcki *et al.* 2014; Low *et al.* 2014; Muiruri, Rainio & Koricheva 2016). Plasticine models were 1 cm long, white, inodorous and shaped to mimic *Eupoecilia ambiguella* and *Lobesia botrana* larvae, the two main lepidopteran pests of grapevine in Europe (Thiery & Moreau 2005). In each vineyard, 30 artificial larvae were fixed on six vine stocks using metal wires (diameter 0.5 mm). Three vine stocks were located at vineyard edges (in the first row), and three vine stocks were located in the centre of the vineyard (30 m from the edge). Artificial caterpillars were exposed to predation during 10 days (between 10th and 20th of June), and the typical marks led by birds were used to assess predator identity (Low *et al.* 2014). Avian predation rates were then estimated as the relative proportion of models showing obvious bill marks left by insectivorous birds after 10 days (Barbaro *et al.* 2014). Other predators recorded included small rodents, arthropods and reptiles, which were excluded from further analyses.

BIRD FUNCTIONAL DIVERSITY

The functional composition of bird communities was computed based on a species–trait matrix of eight life-history traits, including six categorical traits (foraging method, adult diet, nesting site, migration strategy, mean laying date and mean home range size) and two continuous traits (clutch size and body mass; see Table S1, Supporting Information). These selected traits are considered to be key indicators of individual species responses to environmental changes and their provision of pest control services (Philpott *et al.* 2009; Wenny *et al.* 2011; Sekercioglu 2012; Barbaro *et al.* 2014). The computation of functional diversity metrics requires that species abundance is accounted for, multiple traits are considered simultaneously (including both continuous and categorical traits) and all facets of functional diversity are measured (Mason *et al.* 2005; Laliberté, Legendre & Shipley 2015). No single index matches all the criteria; therefore, several complementary indices can be computed,

including functional richness, evenness, divergence and entropy (Moullot *et al.* 2013).

For continuous traits, functional richness (FRic) for a given community is expressed as the convex hull volume of the functional trait space summarized by a principal coordinates analysis (Laliberté, Legendre & Shipley 2015). Functional evenness (FEve) is based on a minimum spanning tree measuring the regularity of trait abundance distribution within the functional space, while functional divergence (FDiv) measures trait abundance distribution within this volume and increases with extreme trait values (Mason *et al.* 2005). Rao's Q measures functional entropy by characterizing species dispersion (distance weighted by abundance) from the functional space centroid, so that a high Rao's Q value indicates a community composed of species functionally different from the mean trait composition (Ricotta & Moretti 2011; Moullot *et al.* 2013). In addition to these multitraits indices, single-trait metrics were calculated using community-weighted mean (CWM) trait values (Laliberté, Legendre & Shipley 2015; Rusch *et al.* 2015). A CWM trait is defined for quantitative traits by the mean value of this trait in a given community, and for qualitative traits by the relative abundance of a given trait modality in each community (Ricotta & Moretti 2011). Pairwise correlations between functional metrics were checked before further analyses.

DATA ANALYSES

We first analysed the effects of local- and landscape-scale heterogeneity and their interactions on bird community variables (i.e. species richness, abundance and functional diversity metrics) using quasi-Poisson GLMs to account for overdispersion in bird count data. There were several levels of non-independence in predation data due to the sampling design that were accounted for in generalized linear mixed model (GLMM) by defining plot identity as random factor. Vine stock identity nested within plots was declared as an additional random factor to account for overdispersion (Grueber *et al.* 2011). Before modelling the effect of landscape heterogeneity and bird diversity on avian insectivory, we compared predation rates at vineyard edges versus interiors. GLMMs were fitted with a binomial error distribution, the response variable being defined as the number of attacked versus non-attacked plasticine caterpillars per vine stock.

As there was no difference between edges and interiors according to a chi-squared test based on log-response ratio, this factor was further discarded. We then used GLMMs with landscape-scale heterogeneity (i.e. % SNH), local heterogeneity (full vs. partial grass cover) and bird community metrics (BCM) as fixed effects. We initially built 17 different sets of full models as follows:

$$Y = b_0 + b_1 \text{BCM} \times (b_2 \text{grass cover} + b_3 \text{SNH}) + \varepsilon$$

where b_i are model parameter estimates, ε is residual error, and BCM is the bird community predictor (see Tables 1 and 2), that is either multitrait metrics FRic, FEve, FDis, Rao's Q or single CWM traits (adult diet, foraging method, clutch size, body mass).

Parameters estimates (\pm SE) of binomial GLMMs that were significantly different from zero were estimated with restricted maximum likelihood (REML). Models were further compared using information theory frameworks based on Akaike's Information Criterion corrected for small samples (AIC_c) to identify the best bird community variable interacting with local and landscape

Table 1. Pearson correlation coefficients for the effects of local- and landscape-scale habitat heterogeneity on bird community metrics

Bird community metrics	SNH	Grass cover
Bird abundance	-0.26 (**)	- (ns)
Bird richness	-0.34 (***)	+ (ns)
FI abundance	+0.36 (***)	- (*)
FI richness	-0.02 (ns)	+ (ns)
FRic	-0.23 (*)	- (ns)
FEve	-0.07 (ns)	+ (ns)
FDiv	-0.49 (***)	+ (**)
RaoQ	-0.54 (***)	+ (**)
CWM.ground probers	+0.06 (ns)	+ (ns)
CWM.ground gleaners	-0.35 (***)	+ (***)
CWM.understorey gleaners	-0.37 (***)	- (ns)
CWM.canopy gleaners	+0.37 (***)	- (***)
CWM.hawkers flycatchers	-0.08 (ns)	- (ns)
CWM.bark foragers	+0.34 (***)	- (*)
CWM.insectivores	+0.09 (ns)	- (**)
CWM.number eggs	+0.35 (***)	- (***)
CWM.body mass	-0.03 (ns)	+ (***)

Landscape heterogeneity refers to the % cover of semi-natural habitats (SNH) within a 500-m-radius buffer around vineyards. Local sward heterogeneity refers to full versus partial grass cover between vine ranks. For grass cover, (-) indicates that the response variable had lower values under partial than full cover and (+) indicates higher value under partial cover. Both tests were based on linear models, and all predictors were scaled before analyses. *P*-values significance thresholds as follows: ns < 0.05 < * < 0.01 < ** < 0.0001 < ***. Codes for bird community metrics as follows: FI, functional insectivores; FRic, bird functional richness; FEve, bird functional evenness; FDiv, bird functional divergence; RaoQ, bird functional entropy; CWM, community-weighted mean traits. Significant correlations with SNH are indicated in bold.

Table 2. Ranking based on ΔAIC_c of best models comparing the relative performance of bird community metrics at fitting predation rates in interaction with local- and landscape-scale habitat heterogeneity

Bird community metrics	AIC_c	ΔAIC_c
FEve	268.68	0
RaoQ	270.98	2.3
CWM.hawkers flycatchers	272.13	3.45
FRic	272.98	4.3
Bird abundance	273.86	5.18
FI abundance	273.86	5.18
FI richness	273.91	5.23
CWM.bark foragers	274.13	5.45
CWM.body mass	274.91	6.23
CWM.ground probers	275.15	6.47
CWM.canopy gleaners	275.32	6.64
CWM.ground gleaners	275.39	6.71
CWM.insectivores	276.8	8.12
CWM.number eggs	277.16	8.48
FDiv	277.93	9.25
CWM.understorey gleaners	278.81	10.13
Bird richness	279.27	10.59

Bold characters refer to the best model (i.e. only model with $\Delta AIC_c < 2$). See Table 1 for bird community metrics codes.

heterogeneity to fit avian insectivory rates. Models were ranked based on their AIC_c , and we estimated model parameters for competing models within a $\Delta AIC_c < 2$ units of the best model with lowest AIC_c (Grueber *et al.* 2011). All model predictors were scaled and centred to allow comparing their relative effects (Schielzeth 2010). We used R packages 'FD' (Laliberté, Legendre & Shipley 2015) for functional metrics, 'LME4' (Bates *et al.* 2015) for mixed models and 'MUMIN' (Barton 2015) for multimodel selection.

Results

BIRD FUNCTIONAL COMPOSITION

Among the 56 bird species recorded, 27 were accordingly classified as 'functional insectivores' (FI). The most frequent functional insectivores recorded were European blackbird *Turdus merula*, blue tit *Cyanistes caeruleus*, common chaffinch *Fringilla coelebs*, blackcap *Sylvia atricapilla*, great tit *Parus major* and common redstart *Phoenicurus phoenicurus*. Altogether, these six species accounted for 26.7% of the total number of individual birds recorded (see Table S1). Total bird abundance and species richness decreased with the percentage of semi-natural habitats in the surrounding 500 m (SNH), but the total abundance of functional insectivores (FI abundance) showed the opposite pattern and increased with landscape heterogeneity (Table 1). Local sward heterogeneity also affected FI abundance, with approximately 15% more functional insectivores in vineyards with full grass cover as compared to vineyards with partial cover alternating with bare ground (Table 1).

Among the multitrait functional metrics, FRic, FDiv and Rao's Q all decreased significantly with landscape heterogeneity, indicating higher trait richness and divergence in vineyard-dominated landscapes than in more heterogeneous landscapes (Table 1 and Fig. 2). Bird communities also tended to display higher functional diversity with partial than with full grass cover between vine ranks (Table 1). Bird functional evenness was uncorrelated to habitat heterogeneity at both local and landscape scales (Table 1). Regarding single-trait indices (CWMs), landscape heterogeneity indicated by higher SNH cover had a positive effect on productive-breeding, canopy-gleaning and bark-foraging insectivores while negatively affecting large ground- and understorey-gleaning granivores or mixed feeders (Table 1). In contrast, local habitat heterogeneity tended to favour larger ground granivores over more productive and smaller canopy insectivores.

BIRD INSECTIVORY

Model selection identified bird functional evenness (FEve) as the bird community metrics best fitting predation rates in interaction with habitat heterogeneity (Table 2). There was no other competing model within two AIC_c units of the best model, but the second best model included functional entropy, Rao's Q index (Table 2). The effect of bird functional evenness on insectivory was significant but depended on habitat heterogeneity at both landscape (FEve \times SNH: estimate \pm SE = 0.57 ± 0.16 ; $\chi^2 = 12.27$; $P < 0.0005$) and local scales (FEve \times grass cover:

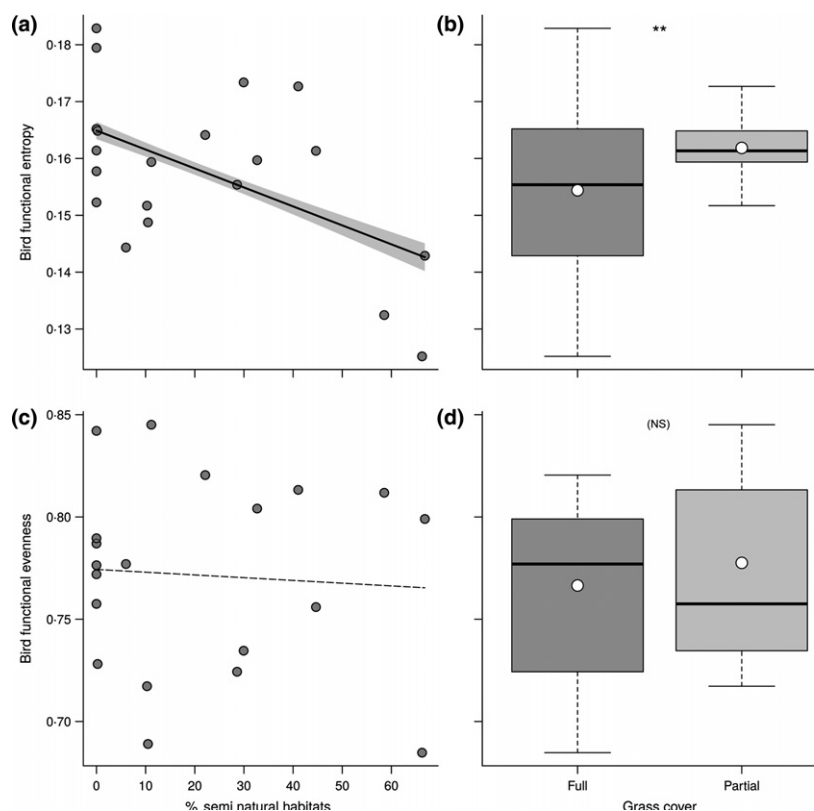


Fig. 2. Effects of landscape (SNH) and local sward heterogeneity on bird functional diversity: (a, b) effects of landscape (a) and local-scale heterogeneity (b) on bird functional entropy (Rao's Q); (c, d) effects of landscape (c) and local-scale heterogeneity (d) on bird functional evenness (FEve). Solid lines and shaded area represent model predictions and corresponding standard errors, respectively. In box plots, horizontal bars represent the median, dots represent means. P -values significance thresholds as follows: ns $< 0.05 < * < 0.01 < ** < 0.0001 < ***$.

estimate \pm SE = 0.69 ± 0.30 ; $\chi^2 = 5.31$; $P < 0.02$). Avian predation increased with bird functional evenness in more heterogeneous landscapes with a large proportion of SNH, but the opposite pattern occurred in more simplified landscapes dominated by vineyards (Fig. 3). At the local scale, avian predation increased with bird functional evenness in vineyards with partial grass cover, while it decreased with bird functional evenness in vineyards with full grass cover (Fig. 4). Except FDiv, functional indices based on multiple traits always ranked higher as predictors of avian predation in model selection than single traits (CWM), even those specifically pertaining to bird foraging method (Table 2).

Discussion

Our study demonstrates that the effect of bird functional diversity on lepidopteran pest predation in vineyards is contingent upon habitat heterogeneity both within (local scale) and around vineyards (landscape scale). Our results therefore have important implications to vineyard management, as we show that both on-field vegetation structure and off-field landscape composition can affect how bird communities drive natural pest control of the main lepidopteran pests in European vineyards.

FUNCTIONAL INSECTIVORY AND LANDSCAPE HETEROGENEITY

Bird insectivory increased with the functional evenness of avian communities but only in more heterogeneous landscape mosaics. Although we did not validate our first prediction of bird functional diversity increasing with landscape heterogeneity, we found partial support for the ‘intermediate landscape complexity hypothesis’ predicting that landscape composition modulates the effect of local management on ecological processes and ecosystem functions (Kleijn *et al.* 2011; Tschardtke *et al.* 2012). A large body of evidence now indicates that landscape heterogeneity (or ‘complexity’ approximated by the percentage of semi-natural habitats in the surrounding matrix) enhances natural pest control (Chaplin-Kramer *et al.* 2011; Tamburini *et al.* 2015; Rusch *et al.* 2016). In vineyards, the ecosystem service of natural pest control is likely provided by a rather small number of functional insectivores whose diet specialization and foraging techniques are expected to allow economically significant reductions in pest insect populations (Jones, Sieving & Jacobson 2005; Jedlicka, Greenberg & Letourneau 2011; Whelan, Sekercioglu & Wenny 2015). Consistently, we found that avian predation rates increased with the relative abundances of functional insectivores and understorey foliage gleaners, as also pointed out by previous studies (Barbaro *et al.* 2014; Bereczki *et al.* 2014; Maas *et al.* 2015). Avian pest control also increased with landscape heterogeneity, but only when bird functional evenness was high (see Fig. 3).

PREDATOR DIVERSITY AND PEST CONTROL

According to meta-analyses, a positive effect of predator diversity on predation rates can emerge from niche complementarity, facilitation among predator species or sampling effects (Letourneau *et al.* 2009; Griffin, Byrnes & Cardinale 2013). While the majority of studies have confirmed an increase in predation rate with predator diversity, several works have also found neutral or even opposite effects, with greater predation in species-poor predator communities (Letourneau *et al.* 2009). These neutral or negative effects may result from antagonistic interactions such as competition or intraguild predation between birds and other guilds of natural enemies (Martin *et al.* 2013; Jedlicka, Letourneau & Cornelisse 2014). The coexistence of many bird functional types promoted by habitat diversity at the landscape scale is expected to increase intraguild competition over functional redundancy or trait complementarity (Luck, Carter & Smallbone 2013). In accordance with this hypothesis, we found that increasing the proportion of semi-natural habitats in vineyard landscapes tended to decrease bird functional diversity, thus mitigating the effect of trait evenness on insectivory on the habitat heterogeneity gradient. While bird functional evenness was the best predictor of predation rates in more heterogeneous landscapes, we assume that insectivory in simplified landscapes was provided by a low number of functional insectivores acting as a biotic insurance in such vineyard-dominated mosaics.

SWARD HETEROGENEITY AND BIRD FORAGING

Together with landscape-scale heterogeneity, sward heterogeneity is an important feature of vineyard management, affecting both insect and bird communities and potentially modifying predator–prey interactions (Arlettaz *et al.* 2012; Vickery & Arlettaz 2012). At the local habitat scale, a partial vegetation cover changed the functional composition of bird communities from canopy foragers towards specialist ground foragers. A denser grass cover actually promotes the abundance of foliage-gleaning insectivores through an increase in food supply, while a sparser cover favours ground-foraging birds by increasing prey accessibility (Browne & Aebischer 2003; Vickery & Arlettaz 2012). Several specialist ground insectivores typical for vineyard agroecosystems, such as Eurasian hoopoe *Upupa epops*, Eurasian wryneck *Jynx torquilla*, woodlark *Lullula arborea*, ciril and ortolan buntings *Emberiza cirilus* and *E. hortulana*, all select microhabitats with patches of bare ground where prey are more accessible even though their abundance is lower (Barbaro & Battisti 2011; Sirami, Brotons & Martin 2011; Arlettaz *et al.* 2012). Large ground granivores including turtle doves *Streptopelia turtur* also favour short and sparse vegetation cover for foraging on wild seeds (Browne & Aebischer 2003). We therefore expected that partial grass cover would overall increase

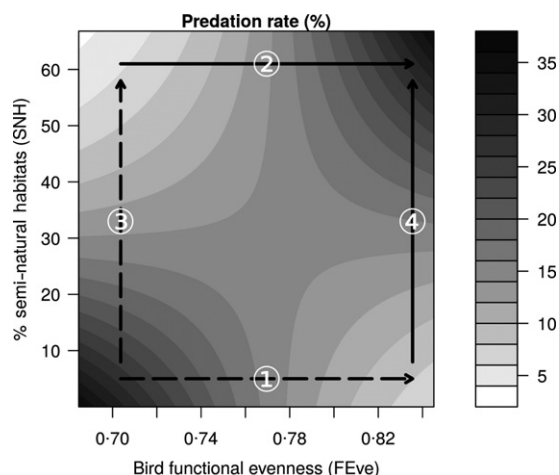


Fig. 3. Interactive effects of bird functional evenness and landscape heterogeneity on avian insectivory. Landscape-scale heterogeneity is approximated by the % cover of semi-natural habitats (SNH) in the surrounding 500 m around vineyards. White to black colour scale represents the increased predation rates predicted by binomial GLMM along crossed gradients of semi-natural habitat amount (SNH) and bird functional evenness (FEve). (1) In simplified landscapes, predation rate decreased with bird functional evenness (dashed line), while (2) it increased with bird functional evenness in heterogeneous landscapes (solid line). (3) Avian predation rate decreased with landscape heterogeneity when bird functional evenness was low (dashed line), while (4) it increased with landscape heterogeneity when bird functional evenness was high (solid line).

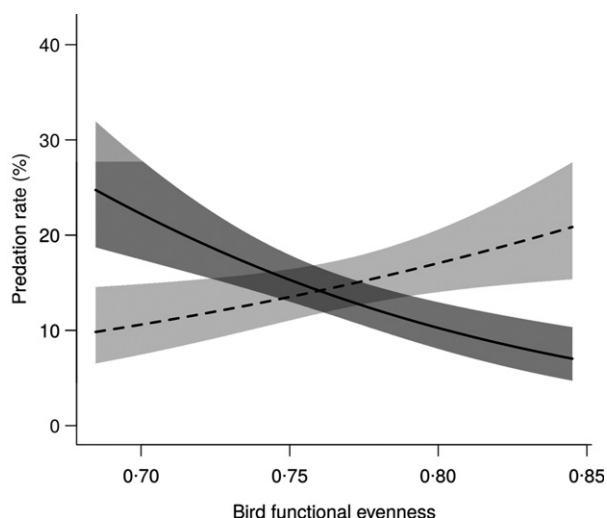


Fig. 4. Interactive effects of bird functional evenness and sward heterogeneity at the local scale (full vs. partial grass cover between vine ranks). Solid black lines and dark grey-shaded areas represent model predictions and corresponding standard errors for full grass cover, and dotted black lines and light grey-shaded areas represent the same for partial grass cover.

avian predation by favouring the complementarity between birds with different foraging strategies. Consistently, we found that avian predation increased with bird functional evenness only in vineyards managed with heterogeneous sward structures (see Fig. 4).

A FUNCTIONAL BASIS FOR BIRD-INDUCED SERVICES

Our study supports the view that a complex interplay between bird species pool, community structure and trait diversity within bird assemblages drives the magnitude of avian predation in vineyards. It also points out the key role of the functional evenness in trait distribution within predator communities to sustain an efficient ecosystem function of pest regulation through trait complementarity (Petchey & Gaston 2006; Hillebrand, Bennett & Cadotte 2008; Crowder *et al.* 2010). How the loss of particular species disrupts ecosystem functions and services is still largely uncertain and constitutes an important area of ecological research (Cadotte, Carscadden & Mirotnick 2011; Mouillot *et al.* 2013), especially when trying to evaluate the intrinsic economic value of biodiversity conservation in agroecosystems (Whelan, Sekercioglu & Wenny 2015). Large-scale biotic homogenization has major functional consequences through the loss of species sharing unique combinations of traits that make them especially relevant to key ecosystem functions and services (Luck, Carter & Smallbone 2013; Lindenmayer *et al.* 2015). The future of bird-induced services in agroecosystems is clearly a major conservation challenge under current global change (Wenny *et al.* 2011; Sekercioglu 2012). Whether these bird-induced services are mainly provided by single opportunistic species (Maas *et al.* 2015; Muiruri, Rainio & Koricheva 2016), specialized guilds of functional insectivores (Jones, Sieving & Jacobson 2005; Barbaro & Battisti 2011) or functionally rich species assemblages is therefore a question of importance in agroecology (Philpott *et al.* 2009; Cadotte, Carscadden & Mirotnick 2011).

SYNTHESIS AND APPLICATIONS

Vineyard agroecosystems have high cultural and economic significance in Europe, with more than 140 millions hL produced on a total production area of 3.4 million ha in 2014. This makes grapevine pest control particularly valuable to wine growers, although natural pest control in vineyards is very sensitive to management intensity (Jedlicka, Greenberg & Letourneau 2011; Rusch *et al.* 2016). Here, we found evidence for pest control by insectivorous birds depending on vineyard management at multiple scales, including local vegetation (e.g. plant diversity, sward height and heterogeneity) and semi-natural habitat cover in the surrounding landscape (woodlands and grasslands), as also suggested by previous studies of predation services in other agroecosystems (De la Mora, García-Ballinas & Philpott 2015; Rusch *et al.* 2015; Tamburini *et al.* 2015). Our study therefore has important implications for both wine growers and policymakers concerned with designing multifunctional landscapes that address both conservation and ecological intensification issues.

As a concluding remark, we suggest that conserving functional communities of insectivorous birds as a biotic

insurance for natural pest control in vineyard-dominated landscapes could be achieved by simultaneously manipulating on-field vegetation (fine-grained habitat heterogeneity) and off-field management of surrounding semi-natural habitats (coarse-grained heterogeneity). Moreover, we also emphasize the increasing importance of a few species of functional insectivorous birds for biocontrol (Jones, Sieving & Jacobson 2005; Maas *et al.* 2015), especially in simplified landscapes dominated by large vineyards where bird diversity is generally low (Pithon *et al.* 2016). Interactions between natural enemy guilds might particularly be affected by changes in the functional diversity of apex predators, through increased intraguild predation (Martin *et al.* 2013; Jedlicka, Letourneau & Cornelisse 2014). More research is needed to examine how such changes in the functional composition of bird communities within vineyard landscapes may have cascading effects on natural pest control services provided by other guilds of natural enemies over time.

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Data accessibility

Source data for 56 bird species abundance recorded during the study and their main life attributes are available online from Table S1. Source data for model predation rates, bird community metrics and habitat heterogeneity variables are available from Dryad Digital Repository at <http://dx.doi.org/10.5061/dryad.3mf45> (Barbaro *et al.* 2016).

References

- Arlettaz, R., Maurer, M.L., Mosimann-Kampe, P., Nusslé, S., Abadi, F., Braunschweig, V. & Schaub, M. (2012) New vineyard cultivation practices create patchy ground vegetation, favouring Woodlarks. *Journal of Ornithology*, **153**, 229–238.
- Barbaro, L. & Battisti, A. (2011) Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). *Biological Control*, **56**, 107–114.
- Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I. & Brockerhoff, E.G. (2014) Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. *Diversity and Distributions*, **20**, 149–159.
- Barbaro, L., Rusch, A., Muiruri, E.W., Gravelier, B., Thiéry, D. & Castagneyrol, B. (2016) Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.3mf45>.
- Barton, K. (2015) Package 'MuMIn'. Model selection and model averaging based on information criteria. R package version 1.15.11.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) lme4: Linear mixed-effects models using Eigen and Eigen. R package version 1.1-10.
- Berezki, K., Ódor, P., Csóka, G., Mag, Z. & Báldi, A. (2014) Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests. *Forest Ecology and Management*, **327**, 96–105.
- Browne, S.J. & Aebischer, N.J. (2003) Habitat use, foraging ecology and diet of Turtle Doves *Streptopelia turtur* in Britain. *Ibis*, **145**, 572–582.
- Buckland, S.T. (2006) Point-transect surveys for songbirds: robust methodologies. *The Auk*, **123**, 345–357.
- Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, **14**, 922–932.
- Crowder, D.W., Northfield, T.D., Strand, M.R. & Snyder, W.E. (2010) Organic agriculture promotes evenness and natural pest control. *Nature*, **466**, 109–112.
- De la Mora, A., García-Ballinas, J.A. & Philpott, S.M. (2015) Local, landscape, and diversity drivers of predation services provided by ants in a coffee landscape in Chiapas, Mexico. *Agriculture, Ecosystems and Environment*, **201**, 83–91.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.
- Griffin, J.N., Byrnes, J.E.K. & Cardinale, B.J. (2013) Effects of predator richness on prey suppression: a meta-analysis. *Ecology*, **94**, 2180–2187.
- Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multi-model inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699–711.
- Hillebrand, H., Bennett, D.M. & Cadotte, M.W. (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, **89**, 1510–1520.
- Jedlicka, J.A., Greenberg, R. & Letourneau, D.K. (2011) Avian conservation practices strengthen ecosystem services in California vineyards. *PLoS ONE*, **6**, e27347.
- Jedlicka, J.A., Letourneau, D.K. & Cornelisse, T.M. (2014) Establishing songbird nest boxes increased avian insectivores and reduced herbivorous arthropods in a Californian vineyard, USA. *Conservation Evidence*, **11**, 34–38.
- Jones, G.A., Sieving, K.E. & Jacobson, S.K. (2005) Avian diversity and functional insectivory on North-Central Florida farmlands. *Conservation Biology*, **19**, 1234–1245.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tscharntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, **26**, 474–481.
- Laliberté, E., Legendre, P. & Shipley, B. (2015) Package 'FD'. Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12.
- Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (2009) Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 573–592.
- Lindenmayer, D.B., Blanchard, W., Tennant, P., Barton, P., Ikin, K., Mortelliti, A., Okada, S., Crane, M. & Michael, D. (2015) Richness is not all: how changes in avian functional diversity reflect major landscape modification caused by pine plantations. *Diversity and Distributions*, **21**, 836–847.
- Low, P.A., Sam, K., McArthur, C., Posa, M.R.C. & Hochuli, D.F. (2014) Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. *Entomologia Experimentalis and Applicata*, **152**, 120–126.
- Luck, G.W., Carter, A. & Smallbone, L. (2013) Changes in bird functional diversity across multiple land uses: interpretations of functional redundancy depend on functional group identity. *PLoS ONE*, **8**, e63671.
- Maas, B., Tscharntke, T., Saleh, S., Dwi-Putra, D. & Clough, Y. (2015) Avian species identity drives predation success in tropical cacao agroforestry. *Journal of Applied Ecology*, **52**, 735–743.
- Mäntylä, E., Klemola, T. & Haukioja, E. (2004) Attraction of willow warblers to sawfly-damaged mountain birches: novel function of inducible plant defences? *Ecology Letters*, **7**, 915–918.
- Mäntylä, E., Klemola, T. & Laaksonen, T. (2011) Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia*, **165**, 143–151.
- Martin, E.A., Reineking, B., Seo, B. & Steffan-Dewenter, I. (2013) Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 5534–5539.
- Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.
- Mols, C.M.M. & Visser, M.E. (2002) Great tits can reduce caterpillar damage in apple orchards. *Journal of Applied Ecology*, **39**, 888–899.

- Mouillot, D., Graham, N.A.J., Vileger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167–177.
- Muiruri, E.W., Rainio, K. & Koricheva, J. (2016) Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia*, **180**, 619–630.
- Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.
- Philpott, S.M., Soong, O., Lowenstein, J.H., Pulido, A.L., Lopez, D.T., Flynn, D.F.B. & DeCleck, F. (2009) Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. *Ecological Applications*, **19**, 1858–1867.
- Pithon, J.A., Beaujouan, V., Daniel, H., Pain, G. & Vallet, J. (2016) Are vineyards important habitats for birds at local or landscape scales? *Basic and Applied Ecology*, **17**, 240–251.
- Ricotta, C. & Moretti, M. (2011) CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*, **167**, 181–188.
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G. & Ekbom, B. (2015) Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic and Applied Ecology*, **16**, 250–259.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D. *et al.* (2016) Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agriculture, Ecosystems & Environment*, **221**, 198–204.
- Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.
- Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology and Evolution*, **21**, 464–471.
- Sekercioglu, C.H. (2012) Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *Journal of Ornithology*, **153**, S153–S161.
- Sirami, C., Brotons, L. & Martin, J.L. (2011) Woodlarks *Lullula arborea* and landscape heterogeneity created by land abandonment. *Bird Study*, **58**, 99–106.
- Tamburini, G., De Simone, S., Sigura, M., Boscutti, F. & Marini, L. (2015) Conservation tillage mitigates the negative effect of landscape simplification on biological control. *Journal of Applied Ecology*, **53**, 233–241.
- Thiery, D. & Moreau, J. (2005) Relative performance of European grapevine moth (*Lobesia botrana*) on grapes and other hosts. *Oecologia*, **143**, 548–557.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P. *et al.* (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.
- Vickery, J.A. & Arlettaz, R. (2012) The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes. *Birds and Habitat: Relationships in Changing Landscapes* (ed. R.J. Fuller), pp. 177–204. Cambridge University Press, Cambridge.
- Wenny, D.G., DeVault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F. & Whelan, C.J. (2011) The need to quantify ecosystem services provided by birds. *Auk*, **128**, 1–14.
- Whelan, C.J., Sekercioglu, C.H. & Wenny, D.G. (2015) Why birds matter: from economic ornithology to ecosystem services. *Journal of Ornithology*, **156**, 227–238.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Full list of bird species recorded in the study and their main attributes.