Foraging traces as an indicator to monitor wild boar impact on ground nesting birds.
Fabrice Roda, Jean-Marc Roda

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Author names and affiliations:

Fabrice Roda
CIRAD, UPR BioWooEB, F-34398 Montpellier, France
757 chemin du Collet Redon, 83136 Rocbaron, France
Email: roda_fabrice@yahoo.fr

Jean-Marc Roda
CIRAD, UPR BioWooEB, 43400 Serdang, France
CIRAD, UPR BioWooEB, F-34398 Montpellier, France
UPM, 43400 Serdang, Malaysia
Email: roda@cirad.fr

Corresponding author:

Fabrice Roda
757 chemin du Collet Redon
83136 Rocbaron
France
Email: roda_fabrice@yahoo.fr

Author contributions:

Conceived and designed the experiments: FR. Analyzed the data: FR and JMR. Contributed analysis tools: JMR. Wrote the paper: FR.

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Foraging traces as an indicator to monitor wild boar impact on ground nesting birds.

Abstract

The successful management of large herbivores requires the monitoring of a set of indicators of ecological change describing animal performance, relative animal abundance, and ungulate impact on habitat. Wild boar populations increases have been spectacular in many countries including France. Wild boars can have a substantial environmental impact on many ecosystem components including birds, but indicators to monitor such impact are currently lacking. In this paper, we examined the usefulness of monitoring the wild boar foraging traces made during their rooting activity to evaluate their impact on ground nesting birds, and developed a simple indicator of kilometric foraging (Ikf) traces found on transects. This study measured the effect of wild boar on bird abundances, controlling for vegetation characteristics (shrub density, time since last clear-cut). Using standardized spot-counts, we found that ground nesting bird abundances were negatively correlated to IkF. Our results showed a significant decrease of 44.7% in ground nesting bird abundances in areas strongly foraged by wild boars. By contrast, abundances of birds depending of ground or tree for food resource, but nesting out of reach of wild boars, were not correlated to foraging traces. We thus conclude that IkF is a simple and suitable indicator that can be used at large scales to monitor wild boar impact on ground nesting birds.

Keywords

ungulates; birds; wild boar; ungulates management; over-abundance

List of abbreviations

AIC: Akaike information criterion
Cut: time since last clear-cut
GN: ground nesting
TN: tree nesting
GF: ground foraging
TF: tree foraging
IEC: indicator of ecological change
Ikf: indicator of kilometric foraging (continuous variable)
Ikf−: areas with low densities of foraging traces
Ikf+: areas with high densities of foraging traces
S: index of shrub density (continuous variable)
S−: areas with low shrub density
S+: areas with high shrub density
Tim: timing of spot-count (early vs. late spring)
Graphical abstract

Indicator of wild boar foraging
1. Introduction

In past decades, the decline of temperate bird species in Western Europe and in North America has attracted much concern (Birdlife International, 2004; Julliard et al., 2004a; Fuller et al., 2007; Gregory & van Strien, 2010; EBCC, 2015). The causes of the observed decline of temperate songbirds are complex. Habitat quality loss may be responsible of the observed decline of forest (Fuller et al., 2007a; Gregory et al., 2007; Quine et al., 2007; Fuller, 2012) and farmland songbirds (Chamberlain & Fuller, 2000; Chamberlain et al., 2000; Voříšek et al., 2010). In addition, climate change poses a threat to some bird species (Julliard et al., 2004b; Jiguet et al., 2007; Gregory et al., 2009).

In parallel to the decline of temperate songbirds, wild ungulate populations increases have been spectacular in many regions of North America (Côté et al., 2004; Rawinski & Square, 2008) and Western Europe (Milner et al., 2006; Massei et al., 2015). The main causes proposed for wild ungulates over-abundance (as defined by Côté et al., 2004) are climate change, the local extermination of natural predator species, supplementary feeding, and changes in agricultural, sylvicultural and game management practices (Flueck, 2000; Milner et al., 2006; Servanty et al., 2009; Massei et al., 2015). For example in Europe, wild boar (Sus scrofa) populations reach historical peaks (Saint-Andrieux et al., 2012; Massei et al., 2015). The impact of over-abundant wild boar on conservation and economic interests include spread of diseases to livestock and people, vehicle collisions, and damage to crops, as well as reduction in plant and animal abundance and richness (Bourcet et al., 2003; Massei & Genov, 2004; Brandt et al., 2006; Vignon & Barbareau, 2008; Barrios-Garcia & Ballari, 2012). As wild boar populations increase in many European countries (Massei et al., 2015), mitigating wild boar impact on environment and economic interests will present a significant challenge. What are the known consequences of large ungulates over-abundance on ecosystems? Numerous studies focus on high deer density impacts on habitats. Deer over-abundance has strong effects on plant communities, vegetation structure, and on abundance of many invertebrate taxa (Fuller & Gill, 2001; Gill & Beardall, 2001; Côté et al., 2004; Joys et al., 2004; Allombert et al., 2005a; Stockton et al., 2005; Dolman & Wäber, 2008; Holt et al., 2011; ONF, 2013). Such changes in the woodland ecosystem affecting food and safe nesting availability are responsible for the negative cascading effects on songbird abundance and biodiversity (McShea and Rappole, 2000; Allombert et al., 2005b; Hewson et al., 2011; Holt et al., 2011; Martin et al., 2011). As omnivorous mammals, wild boars can have a substantial environmental impact and may affect many ecosystem components (Massei and Genov, 2004). Their rooting activity can remove the herbaceous cover (Bratton, 1975; Howe et al., 1981; Carpio et al., 2014a), and cause a decrease of tree regeneration (Gomez et al., 2003). Wild boars negatively affect rodents by direct predation on juveniles (Schley and Roper, 2003) or/and competition for food resource (Focardi et al., 2000; Carpio et al., 2014a). Wild boar over-abundance has cascading effects on threatened predators such as wildcat (Felis silvestris) by reducing rodent prey availability (Lozano et al., 2007). Previous studies on wild boar-birds interactions in their native range focused mainly on game bird species (Massei & Genov, 2004). Wild boar predated capercaillie (Tetrao urogallus) and hazel grouse (Tetrastes bonasia) nests (Saniga, 2002; Saniga, 2003) and simulated nests of red-legged partridge (Carpio et al., 2014b). As over-abundant wild boar preys on everything on the ground, their negative effects both in their native and introduced range are thus well established (Barrios-Garcia & Ballari, 2012).

To manage wild ungulates ecological footprint, it is necessary firstly to evaluate population size and secondly to precisely measure the ungulates impact through environmental indices. Monitoring changes in these indices provides a basis for setting management objectives (Morellet et al., 2007). Large herbivores populations are usually controlled through hunting in Europe (Milner et al., 2006;
Massei et al., 2015). Capture-Mark-Recapture methods (CMR) provide an efficient approach to estimate reliably population size, but are extremely time-consuming and expensive when applied to large herbivores (Buckland et al., 2000). Distance sampling methods are less time-consuming but suffer from less accuracy and precision (Buckland et al., 2000; Thomas et al., 2010). Both methods do not provide any functional information on the population-habitat system, as population size per se does not provide information on the environment. In addition, the primary concern for ungulate managers is often to prevent over-abundance of herbivore populations (Mysterud, 2006; Nichols & Williams, 2006) rather than predicting accurately how many animals may be harvested or not. Researchers have recently developed tools for managing ungulate populations, which are based on the monitoring of a set of indicators of ecological change (“IEC”; Cederlund et al., 1998; Morellet et al., 2007). An IEC is an easily measured parameter, sensitive to changes in the relationship between the population and its resources and habitat (Cederlund et al., 1998; Dale & Beyeler, 2001). Morellet et al. (2007) suggested tracking over time the variations of at least three categories of IECs: one describing animal performance, another describing herbivore impact on environment, and the last describing relative animal abundance. A set of IECs has been first developed for deer management (Morellet et al., 2007), but such a set of indicators is currently lacking for wild boar. Recently, Acevedo et al. (2007) developed a method describing wild boar abundance based on the frequency of fecal droppings. However, IECs describing wild boar impact on fauna, flora, biodiversity and habitat are currently lacking. The main objective of this study was thus to find such an IEC to monitor the impact of wild boar on avifauna.

We made the hypothesis that H1) wild boar preying activity should disturb ground nesting birds and thus decrease their abundances in highly foraged areas. Tree nesting birds are out of reach of wild boars, so we hypothesized that H2) tree nesting birds abundances should not negatively correlate with wild boar foraging activity. As wild boars may have an impact on birds by food competition, we investigated H3) the impact of wild boars on birds depending of ground for food resource, but nesting out of reach of wild boars.

2. Material and methods

2.1 Study area

The forest massif of Morières / Siou Blanc is situated in southeastern France (8638-ha forest area; altitude 500-650m, Figure S1), in an area with low human density, within which, there are only a few isolated houses. The climate of Morières / Siou Blanc is Mediterranean, with hot and dry summers, mild winters and moderately rainy autumns and springs (mean maximal temperature in July = 27,6°C; mean minimal temperature in July = 19,4°C; maximal annual mean = 18,8°C; minimal annual mean = 12,1°C; mean precipitation in July = 5,6 mm; annual mean 613,4 mm) (Météo France). The forest massif exhibits Mediterranean vegetation, typical of southeastern France. It displays various profiles of vegetation, according to forest management stages. It is a coppice forest, with holm oak (Quercus ilex), downy oak (Quercus pubescens) and a large diversity of shrubs. Some areas are dominated by various pines (Pinus spp.) and by xeric species of scrubs (Rosmarinus officinalis, etc.). Numerous stands contained a mix of pines and oaks.

Sport hunting is an important activity in this forest massif, mainly focused on big game species, especially wild boar. Wild boar abundance varies significantly throughout the massif, with high numbers harvested (6,3 wild boars killed/km²/year). In contrast, roe deer (Capreolus capreolus) is scarcer (0,9 animals killed/km²/year), and red deer (Cervus elaphus) is absent. A small cluster of approximately 50 fallow deer (Dama dama), has been recently introduced by game managers. Livestock animals are absent in the prospected area.
Figure S1: Location of the study area in southeastern France, showing layout of forest massif Of Siou Blanc les Morrières.
2.2 Sampling protocol

Twenty-six stations were randomly selected. They are evenly spread over the whole forest massif, without prior knowledge of the vegetation, structure or bird communities. Ground visits were organized during the winter season and the positions of the stations were recorded using GPS to allow their subsequent localisation. The stations were in the main body of the forest of Morrières / Siou Blanc and were therefore surrounded on all sides by woodlands. Around each station, a 1 km survey transect was set-up to search for wild boar foraging traces. The survey routes were along pre-existing paths or forest roads of 1-5m width (allowing the possibility for cars or people to enter to the different places).

Each survey route was divided into 100m-length segments, yielding 10 segments per transect. In each segment, the presence of wild boar foraging traces was recorded, which allowed the derivation of a simple indicator of kilometric foraging (Ikf, a continuous variable), that is, the number of segments with wild boar foraging traces/10 segments. This methodology gives an index derived on the frequency of occurrence (see a similar methodology based on fecal droppings in Acevedo et al., 2007). When signs of rooting activity were seen and occupied a contiguous ground area larger than 2m², the segments were considered as positive. Stations with Ikf ranging from 0 to 0,5 were considered as low wild boar traces (Ikf-). Stations with Ikf from 0,6 to 1 were considered as high wild boar traces (Ikf+). These two level factor were used for GLM analysis (see below, statistics section). Two measures of Ikf were made during spring for each station, between 1st April and 30th May 2012. We measured Ikf the same days as bird surveys (see 2.3). We found 25 counts with low densities of wild boar foraging traces (IkF-), and 27 counts with high wild boar foraging traces (IkF+).

Along each survey route, we measured variables related to habitat structure, viz., tree cover, density of shrub cover, average tree and shrub heights. Based on results of previous bird studies (see below "Vegetation data" section ), we expected these variables to play an important role.

2.3 Bird survey

Spot-counts were all done by the same observer (FR). Counts were carried out in each plot during two visits in spring 2012 ; point-count times were separated by an interval of at least four weeks to detect both early and late breeding birds (1st-15th April and 15th-30th May), following the recommendations of the French Breeding Bird Survey of the National Museum of Natural History (MNHN, 2012; Jiguet et al., 2012). Counts were performed within 1-4h after sunrise. Point-count stations (n = 26) were positioned a minimum of 500m apart to avoid overlap of bird counts. To minimize a potential edge effect (Ries and Sisk, 2004), the center of all study plots were situated at least 100m from the edge of forest alleys. We used 100m fixed-radius point-counts that lasted 5 minutes to allow for a good estimation of relative bird abundances, following the methodology detailed in Blondel et al., 1970 and Jiguet et al., 2012. Repeating point-counts throughout the breeding season improved estimation of species richness and relative abundances of birds (Dettmers et al., 1999; Drapeau et al., 1999; Bonthoux and Balent, 2012). Points were recorded in the reverse order during the second count to avoid introducing temporal bias between different stations. Since all of the plots were located in core forest habitats with low visibility, birds were mostly detected through their song. Individuals could be distinguished when several birds continuously sang at different locations in the plot.

We excluded observations of raptors, i.e., Golden Eagle (Aquila chrysaetos), Bonelli’s Eagle (Aquila fasciata), Short-toed Snake Eagle (Circaetus gallicus), Peregrine Falcon (Falco peregrinus), Common Kestrel (Falco tinnunculus), Eurasian Sparrowhawk (Accipiter nisus), corvids (Corvus corrax and Corvus corone), Common Cuckoo (Cuculus canorus), and Eurasian
Woodcock (Scolopax rusticola) as these species were poorly surveyed by the method used and/or have life cycles that make them irrelevant to the objective of the study. Game birds (Alectoris rufa, and Phasianus colchicus) were not recorded since their presence in a particular station may have been due to game releases in the area.

To test the hypothesis that the wild boar impact on birds may result of direct predation, we established a classification system that grouped the bird species encountered during the study into two guilds according to the nesting habitat (i.e., ground nesting vs. tree/shrub nesting birds). To test the hypothesis that wild boar may impact birds through food competition, birds were grouped into two guilds according to ground dependence for foraging and gleaning (i.e., ground foraging vs. tree foraging birds). Ground nesting birds were separated from ground foraging and tree foraging guilds to avoid potential overlap of effects (i.e., predation and food competition). Location of the nest-site were taken from literature (Gregory et al., 2007; Flitti et al., 2009) and our own observations (See Table S1). Four indicators were derived: an indicator for ground nesting birds (GN, n=201 birds), and an indicator for tree nesting birds (TN, n=339 birds), an indicator for ground foraging birds (GF, n=234 birds) and an indicator for tree foraging birds (TF, n=105 birds).

At the bird community level, we used species diversity as bird community indicator. Species diversity was calculated using the Shannon index. The Shannon index reflects the number of different species in a community and simultaneously takes into account how evenly the individuals are distributed among those species (Lyashevska & Farnsworth, 2012).

2.4 Vegetation data

This study measured the effect of wild boar on birds, controlling for vegetation characteristics (shrub density, time since last clear-cut). Vegetation data were collected during spring 2012, after each bird count session. Measurements were taken at three sampling areas at each point-count station, thus resulting in 78 sampling points. One was located at the point-count station itself, the other two at random distances from the station (<50m). Mean values were calculated for each variables listed. Shrub layer density of vegetation layer (0-1m) was estimated using a pole graduated into 10cm sections and using a protocol adapted from Holt et al. (2011). The number of sections obscured by vegetation was recorded when viewed from a distance of 10m. An index of shrub density (S, a continuous variable) was derived using the number of segments obscured/10 segments, from 0 to 1. We used these scores to define two classes of shrub layer density: values equal or smaller than 0,5 were considered as "low density" (S-), those equal or greater than 0,6 as "high density" (S+); this two level factor was used for GLM analysis (see below, statistics section).

As avian community structure is largely determined by the growth stage and associated structural characteristics of vegetation (Fuller et al., 1989), vegetation age was controlled in each plot, using local forest management archives. Time since last clear-cut (Cut) was used as a continuous variable for statistical purpose (see below, statistics section).

As cervids are known to have an impact on birds (see Allombert et al., 2005b; Holt et al., 2011; Martin et al., 2011), signs of browsing were carefully searched in each sampling area. We considered only shrub species or woody plants because we could not, with herbaceous species, distinguish deer browsing from that of lagomorphs present in the study area. We recorded the browsing pressure by assessing the number of eaten twigs versus all available twigs at a height <1.80 m, following a methodology similar to those described elsewhere (Picard, 1988; Chevrier et al., 2012). A “browsing sign” is one bite by the animal on the tree, being evident as a fresh cut on the twigs. As the browsing pressure was <1% in all the sampled plots, the cervids impact on the avifauna was considered negligible in this study. All the assessments were done by the same person (FR).
Table S1
Classification of species in relation to foraging and nesting dependence

<table>
<thead>
<tr>
<th>Species acronym</th>
<th>Species name</th>
<th>Ground or Tree/shrub dependence</th>
<th>Migration strategy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Nesting</td>
<td>Foraging</td>
</tr>
</tbody>
</table>

**(a) Species**

<table>
<thead>
<tr>
<th>Species acronym</th>
<th>Species name</th>
<th>Ground or Tree/shrub dependence</th>
<th>Migration strategy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cya cae (n=55)</td>
<td>Eurasian Blue Tit (<em>Cyanistes caeruleus</em>)</td>
<td>Tree/shrub</td>
<td>Tree/shrub</td>
</tr>
<tr>
<td>Eri rub (n=69)</td>
<td>Robin (<em>Erithacus rubecula</em>)</td>
<td>Ground</td>
<td>Ground</td>
</tr>
<tr>
<td>Fri coe (n=111)</td>
<td>Common Chaffinch (<em>Fringilla coelebs</em>)</td>
<td>Tree/shrub</td>
<td>Ground</td>
</tr>
<tr>
<td>Lus meg (n=51)</td>
<td>Nightingale (<em>Luscinia megarhynchos</em>)</td>
<td>Ground</td>
<td>Ground</td>
</tr>
<tr>
<td>Par maj (n=50)</td>
<td>Great Tit (<em>Parus major</em>)</td>
<td>Tree/shrub</td>
<td>Tree/shrub</td>
</tr>
<tr>
<td>Phy bon (n=81)</td>
<td>Western Bonelli’s Warbler (<em>Phylloscopus bonelli</em>)</td>
<td>Ground</td>
<td>Tree/shrub</td>
</tr>
<tr>
<td>Syl atr (n=43)</td>
<td>Eurasian Blackcap (<em>Sylvia atricapilla</em>)</td>
<td>Tree/shrub</td>
<td>Ground</td>
</tr>
<tr>
<td>Syl mel (n=26)</td>
<td>Sardinian Warbler (<em>Sylvia melanocephala</em>)</td>
<td>Tree/shrub</td>
<td>Ground</td>
</tr>
<tr>
<td>Tur mer (n=34)</td>
<td>Blackbird (<em>Turdus merula</em>)</td>
<td>Tree/shrub</td>
<td>Ground</td>
</tr>
</tbody>
</table>

**(b) Guilds**

<table>
<thead>
<tr>
<th>Guild</th>
<th>Species name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground Nesting  (GN, n=201)</td>
<td>Common Nightingale; Robin; Western Bonelli’s warbler</td>
</tr>
<tr>
<td>Tree Nesting (TN, n=339)</td>
<td>Blackbird; Common Chaffinch; Great Tit; Eurasian Blackcap; Eurasian Blue Tit; Sardinian warbler</td>
</tr>
<tr>
<td>Ground Foraging (GF, n=234)</td>
<td>Blackbird; Common Chaffinch; Eurasian Blackcap; Sardinian warbler</td>
</tr>
<tr>
<td>Tree Foraging (TF, n=105)</td>
<td>Great Tit; Eurasian Blue Tit</td>
</tr>
</tbody>
</table>
2.5 Statistics

We tested for the effects of 1) wild boar foraging (Ikf), 2) shrub cover (S), 3) timing of spot-counts (Tim) and 4) time since last clear-cut (Cut) (the factors of variation) on birds abundances, and species diversity (the dependent variables) using general linear models (GLM). For the count data (bird abundances), each model was tested assuming normal (Gaussian) and Poisson error. We selected the best model using the Akaike Information Criterion (AIC). However, when the AIC of two competing models differed by less than 2, we examined the residual sum of squares and retained the simplest model in line with the rules of parsimony. We checked for the homoscedasticity and normality assumptions of residuals. Raw data were not transformed, and real birds counts were used throughout the paper. Timing of spot-count was entered as a two-level factor (early vs. late) in all the models. Wild boar foraging and shrub cover were entered as a two-level factors (Ikf- vs. Ikf+; and S- vs. S+, respectively) to investigate potential interactions between factors. Entering wild boar foraging and shrub cover as continuous covariates led to the same conclusions. Time since last clear-cut was entered as a continuous covariate (Cut) in all models. Birds were grouped in functional guilds (See Table S1). We fitted several models including interactive effects of Ikf, S, Tim and Cut. As a control of potential bias in our study, we tested the effects of 1) S and 2) Tim (the factors of variation) on Ikf (the dependent variable) using GLM. Statistical evaluation was carried out with the “Statistica” software using the functions “GLM” (normal error) or “GLZ” (poisson error). Best results were obtained assuming normal error. Nine bird species that were at least observed in one third of point-counts, were included in statistical analysis. All results are expressed as mean ± SEM. Differences were considered significant at P < .05.

3. Results

3.1 General results

Wild boar foraging traces were observed in all surveyed transects. Maximum value of wild boar indicator of kilometric foraging (Ikf) was of 1 with a high mean value of 0,60 ± 0,03, indicating a relatively strong pressure of wild boar foraging in the study area considered as a whole. Twenty-five spot-counts showed few wild boar traces (Ikf-), and 27 showed many traces (Ikf+, see methods section). GLM analysis showed no relationships between Ikf and timing of spot-counts (Tim) or shrub cover (S) (Adjusted R²=0,02; F=1,31; p=0,28). We analyzed the abundances of 9 bird species and 520 individuals (Table S1). Counts led to an average of 3,9 ± 0,3 SE ground nesting birds (range 0-8); 6,5 ± 0,3 SE tree nesting birds (range 3-13); 4,5 ± 0,3 SE ground foraging birds (range 1-9); and 2,0 ± 0,2 SE tree foraging birds per spot (range 0-7).

3.2 Wild boar impact on birds

We tested the effects of Ikf, Tim, S and Cut on the abundance of ground nesting birds. Abundances of TN, GF and TF birds were also tested as supplementary variables. The best model included the variables Ikf, S and Tim; Cut, TN, GF and TF were rejected as explanatory variables (Table 1). The observed changes were well explained by the GLM and were very statistically significant (Adjusted R²=0,70; F=17,89; p<10⁻⁶). We found that the abundance values of GN birds were negatively correlated with Ikf (Figure 1a). Entering IkF as a two-level factor showed that there was a significant decrease of 44.7% in ground nesting birds abundances in areas strongly foraged by wild boars (Figure S2). GLM revealed the role of Ikf as being the main factor driving bird abundance changes, and Tim and S as being secondary factors, in this order (Table 2). Test of categorical variables interactions as explanatory variables were not significant (Table 2). The effect of Tim showed that birds were more numerous in late spring. We observed that the negative effect of wild boars on birds abundances was slightly greater in early spot-counts than late, but this result
Figure 1: Variations of forest bird mean abundances in relation to wild boar foraging (Ikf). Predicted trends are presented as black lines with 95% confidence intervals (dashed lines). Bars indicate the standard error of mean. (a) ground nesting (GN) birds (b) tree nesting (TN) birds (c) ground foraging (GF) birds (d) tree foraging (TF) birds.
Table 1: Candidate models explaining ground nesting birds abundance, with the Akaike information criterion values (AIC) and the selected variables: wild boar foraging (Ikf), timing of spot-count (Tim), shrub density (S), time since last clear-cut (Cut), tree nesting birds abundance (TN), ground foraging birds abundance (GF), tree foraging birds abundances (TF). The interactions between wild boar foraging and timing (IkF*Tim), wild boar foraging and shrub density (IkF*S), wild boar foraging, timing and shrub density (IkF*Tim*S) were also tested, but gave higher scores of AIC (data not shown). Bold characters indicate the selected model.

<table>
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<tr>
<th>Guild</th>
<th>selected variables</th>
<th>AIC</th>
<th>SS</th>
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<tr>
<td>Ground Nesting (GN)</td>
<td>Ikf</td>
<td>Tim</td>
<td>S</td>
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Figure S2: Mean abundances of ground nesting (GN) in relation to wild boar foraging. Ikf(-) areas moderately foraged by wild boars; Ikf(+) areas strongly foraged by wild boars. Lines indicate standard error of mean. Results are highly significant (p<10^{-6}); see Table 2 and statistical analysis.
Table 2: β coefficients and statistical parameters of the most parsimonious GLM model to explain ground nesting (GN) birds abundance using wild boar foraging traces (Ikf), Timing (Tim) and shrub density (S) as predictors. Bold characters indicate statistically significant results.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Level of effect</th>
<th>Column</th>
<th>GN param.</th>
<th>± SE</th>
<th>GN t</th>
<th>p</th>
<th>GN β</th>
<th>± SE</th>
</tr>
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<tbody>
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<tr>
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</tbody>
</table>

Figure S3: mean abundances of ground nesting (GN) in relation to wild boar foraging and shrub density. IkF(-) areas moderately foraged by wild boars; IkF(+) areas strongly foraged by wild boars. Black filled circles indicate areas with high density of shrubs; Open grey squares indicates areas with light shrub density. Lines indicate standard error of mean. Results are highly significant (p<10^{-6}); see Table 2 and statistical analysis.
was not statistically significant. Shrub cover was positively correlated to ground nesting birds abundances. The negative effect of Ikf on birds abundances was marginally greater in S- than in S+ areas, but this result was not statistically significant (Figure S3). Mean values of GN birds in relation to hypothesis decomposition are summarized in Table S2.

Table S2
Mean values of GN birds in relation to hypothesis decomposition.

<table>
<thead>
<tr>
<th>Cell number</th>
<th>IkF</th>
<th>Tim</th>
<th>S</th>
<th>GN means</th>
<th>GN ± SE</th>
<th>GN -95% conf. Int.</th>
<th>GN +95% conf. Int.</th>
<th>N</th>
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<tbody>
<tr>
<td>1</td>
<td>(-)</td>
<td>early</td>
<td>(+)</td>
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<td>early</td>
<td>(-)</td>
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<td>(-)</td>
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<td>(+)</td>
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</tr>
<tr>
<td>4</td>
<td>(-)</td>
<td>late</td>
<td>(-)</td>
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<td>0.3</td>
<td>4.4</td>
<td>5.8</td>
<td>11</td>
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<td>(+)</td>
<td>early</td>
<td>(+)</td>
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<tr>
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<td>(+)</td>
<td>early</td>
<td>(-)</td>
<td>1.2</td>
<td>0.3</td>
<td>0.5</td>
<td>1.8</td>
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</tr>
<tr>
<td>7</td>
<td>(+)</td>
<td>late</td>
<td>(+)</td>
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<td>3.6</td>
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<td>6</td>
</tr>
<tr>
<td>8</td>
<td>(+)</td>
<td>late</td>
<td>(-)</td>
<td>3.0</td>
<td>0.4</td>
<td>2.1</td>
<td>3.9</td>
<td>6</td>
</tr>
</tbody>
</table>

Table S3
Model selection for TN, GF and TF birds
When two models had similar AIC and SS Residual scores, the most parsimonious model was chosen (see methods).

<table>
<thead>
<tr>
<th>Guild</th>
<th>selected variables</th>
<th>AIC</th>
<th>SS Residual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree Nesting (TN)</td>
<td>Ikf  Tim S Cut Tim<em>S Ikf</em>Tim*S</td>
<td>220.9</td>
<td>225.5</td>
</tr>
<tr>
<td>Ground Foraging (GF)</td>
<td>Ikf  Tim S Cut Tim<em>S Ikf</em>Tim*S</td>
<td>215.3</td>
<td>158.2</td>
</tr>
<tr>
<td>Tree Foraging (TF)</td>
<td>Ikf  Tim S Cut Tim<em>S Ikf</em>Tim*S</td>
<td>169.5</td>
<td>77.9</td>
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</table>
We tested the effects of Ikf, Tim, S and Cut on the other guilds. Results of model selection are summarized in Table S3. By contrast to ground nesting birds, abundances of birds belonging to tree nesting (Figure 1b) or ground foraging (Figure 1c) guilds were not well explained by IkF or the other studied variables; the observed changes were not statistically significant (Adjusted R²=0.05; F=1.4; p=0.24; Adjusted R²=0.01; and F=1.1; p=0.40, respectively). The best model describing the tree foraging birds abundances included Ikf and Tim as explanatory variables (Table S3), but the observed changes were barely significant (Adjusted R²=0.12; F=2.0; p=0.07). However, we noted that tree foraging birds slightly tended to be more numerous in areas strongly foraged by wild boars, a not significant result (Figure 1d).

We then tested the effects of Ikf, Tim, S and Cut on bird species diversity. The best model describing species diversity included the variables Tim, IkF*S, Tim*S; Cut was rejected as an explanatory variable (Table S4). The observed changes in species diversity were statistically significant (Adjusted R²=0.33; F=4.6; p<10⁻³). We found that the main factor affecting bird species diversity was the interaction of IkF*S (Figure 2, Table S5).

The present data indicate that, in accordance with H1, GN birds were less abundant in areas strongly foraged by wild boars (Figure 1a). Thus, in accordance with H2, TN birds abundance was not affected by wild boar foraging (Figure 1b). In addition, GF birds abundance was not correlated to wild boar foraging (H3, Figure 1c).

![Figure 2: Variations of bird species diversity (Shannon) in relation to wild boar foraging (Ikf) and shrub density. Predicted trends are presented as black lines with 95% confidence intervals (dashed lines). Bars indicate the standard error +mean. (a) bird species diversity in areas with low shrub cover. (b) bird species diversity in areas with dense shrub cover.](image-url)
Model selection for species diversity

When two models had similar AIC and SS Residual scores, the most parsimonious model was chosen (see methods).

**Table S5**

$\beta$ coefficients and statistical parameters of the most parsimonious GLM model to explain species diversity using wild boar foraging traces (IkF), Timing (Tim) and shrub density (S) as predictors

<table>
<thead>
<tr>
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<th>Level of effect</th>
<th>Column</th>
<th>Sp. div. param.</th>
<th>± SE</th>
<th>Sp. div. t</th>
<th>Sp. div. p</th>
<th>Sp. div. $\beta$</th>
<th>± SE</th>
</tr>
</thead>
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<td>Intercept</td>
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<td>0.0</td>
<td>-1.92837</td>
<td>0.060277</td>
<td>-0.24</td>
<td>0.13</td>
</tr>
<tr>
<td>S</td>
<td>(+)</td>
<td>3</td>
<td>0.1</td>
<td>0.0</td>
<td>1.27066</td>
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<td>0.16</td>
<td>0.12</td>
</tr>
<tr>
<td>IkF</td>
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<td>0.1</td>
<td>0.0</td>
<td>1.33765</td>
<td>0.187885</td>
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<td>0.13</td>
</tr>
<tr>
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<td>1.91937</td>
<td>0.061437</td>
<td>0.24</td>
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<tr>
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<td>0.609837</td>
<td>0.06</td>
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4. Discussion and conclusions

4.1. Wild boar foraging as an indicator of ecological change

Surprisingly, the use of foraging traces as an indicator of wild boar impact on ground nesting birds has never been tested until now (Massei & Genov, 2004; Ballari & Barrios-Garcia, 2012). We found that wild boar foraging traces provided a simple indicator of ground nesting birds abundance. Our results evidenced the usefulness of this method since it was highly correlated with GN birds abundances, but not with other avian guilds (tree nesting or ground foraging birds). The protocol described in this study has numerous advantages. First, the measurements do not depend on biological experts for birds species determination: in other words, anyone can perform an inventory of wild boar foraging traces. Wild boar foraging traces are easily spotted, and the probability of detection is likely constant among different observers using a standardized protocol. Second, wild boar foraging traces are rapidly measured; this may prove useful for monitoring programs designed to track annual changes of wild boar environmental impact on ground ecosystems at large spatial scales. Third, measuring wild boar foraging traces is less climate dependent than measuring bird abundances. Finally, the monitoring of wild boar impact on the avifauna do not requires the previous knowledge of wild boar population size.

Understanding and measuring the environmental impact of wild ungulates in forest ecosystems remains a challenge for researchers and wildlife managers. In practice, for management to succeed, clear goals are required and the success of their application must be evaluated (Morellet et al., 2007). The goal will often be a compromise such as maximising the revenue from hunting while minimising damage to forestry/biodiversity (Williams et al., 2002; Nichols & Williams, 2006). Wildlife population trends are often assessed by species counts; surveillance monitoring frequently requires several years to amass enough data to provide strong evidence of a decline in state before action is taken. Species sampling methods remain labor intensive and time-consuming, and may be subject to many biases (Kéry & Schmidt, 2008; Renwick et al., 2012). As a result, there is an increasing demand from policy makers to improve management by incorporating relevant indicators that are simple, reliable and rapidly assessed. By recording a set of IECs, the aim is to achieve management objectives, rather than exert a routine surveillance monitoring (Cederlund et al., 1998; Dale & Beyeler, 2001; Morellet et al., 2007). To manage wild ungulates, it is thus suggested to track over time the variations of at least three categories of indicators of ecological changes (Morellet et al., 2007): one describing animal performance, another describing herbivore impact on environment, and the last describing relative animal abundance.

As pointed by Dale and Beyeler (2001), the focus of ecological management programs becomes narrow by selecting only one or few indicators, and may lead to oversimplified understanding of the ecological interactions involved; the management of large ungulates is greatly improved by the recording of a set of indicators (Morellet et al., 2007). To avoid poorly informed management decisions, indicators should take into account multiple levels in the ecological network in order to effectively monitor the multiple levels of complexity of ecological systems (Dale & Beyeler, 2001; Niemeijer & de Groot, 2008). Thus, a key challenge is to find a mix of measures which give easily identified signals, can be used to track the ecological conditions at reasonable cost, and cover the spectrum of ecological variation. The monitoring of our indicator of wild boar foraging responds to these criteria; and thus managers dispose rapidly and easily of a diagnostic of wild boar potential environmental impact on avifauna. However, if management interventions are required (i.e., if the manager estimates that wild boar impact on ground nesting birds may conflict with conservation interests), the accuracy of management will be greatly improved by studies carried out to estimate wild boar population size and trends. As such tools of wild boar abundance do already exist, based on fecal drops (Acevedo et al., 2007), one goal of this study (to complete the set of indicators for wild boar management) was fulfilled. However, to be fully acknowledged as a new IEC, our
 indicator should be ideally tested over a long period of time, in reference localities where true wild
boar population size is known (Dale & Beyeler, 2001; Morellet et al., 2007). With a set of IECs, one
can envisage an adaptive management program (as defined by Nichols & Williams, 2006) of wild
boar game harvest compatible with bird conservation. The final step is then to set new hunting
quotas with the aim of provoking an adjustment in the population-habitat system in order to
approach the predefined goals. At least during the first years of monitoring, this is equivalent to a
trial-and-error process or adaptive management (Nichols & Williams, 2006; Morellet et al., 2007).

4.2. Effects of wild boar foraging on birds abundance

To our knowledge, our study is the first to correlate bird abundances to an index based on the
frequency of wild boar foraging traces. Our results showed a significant decrease of 44.7% in
ground nesting birds abundances in areas strongly foraged by wild boars; in contrast, tree nesting
birds (out of reach of large ungulates) were not affected by wild boar gleaning. This result was
expected since ground nesting birds are highly impacted by other over-abundant ungulates
(Allombert et al., 2005b; Holt et al., 2011), and wild boars are known to be highly opportunistic
mammals that prey on anything near the ground: depredations on birds and nests (Saniga, 2002;
Saniga, 2003; Schaefer, 2004; Giménez-Anaya et al., 2008; Carpio et al., 2014b), reptiles and
amphibians (Jolley et al., 2010), small mammals (Lozano et al., 2007; Wilcox & van Vuren, 2009),
and other fauna and flora communities are substantial (see for review Barrios-Garcia & Ballari,
2012). The general assumption that all clutches of birds that nest on the ground represented
potential prey for wild boars is thus probably true. This predation effect may explain the observed
changes in bird distribution, as predation risk is known to influence prey-birds use of space
(Thomson et al., 2006; Cresswell, 2008). We noted a cross-effect of wild boar foraging and habitat
on birds, i.e. the effects of wild boar foraging on species diversity were more important in areas
with low shrub cover. Other studies pointed that the density of potential nests and predation rates is
dependent on vegetation structure complexity and that foliage density near the nest may reduce
predation impact (Martin et al., 1988; Chalfoun & Martin, 2009). In addition to resource
competition, predation risk is an important factor determining spatial distribution of birds (Suohonens,
1993) and offspring success (Martin, 1996; Thomson et al., 2006; Chalfoun & Martin, 2007).
Interestingly, GN birds abundances were influenced by the timing of spot-count. As two of three
species composing the GN birds guild are long-migrant species, this result is not surprising. Further
research is needed to investigate the potential interactions between migration strategy and wild boar
impact, i.e., if long-migrant birds are more impacted than partial-migrants.

We then explored the hypothesis that wild boar may compete with ground foraging birds for food
resource. Previous studies showed that wild boars negatively impacted rodents populations as a
result of direct competition for seeds (Focardi et al., 2000) or legumes (Carpio et al., 2014a).
Although wild boars are omnivorous and prey invertebrates, diet consist mainly of plant matter
including above-ground green material (Fournier-Chambrillon et al., 1995; Baubet et al., 2004).
The most obvious direct effect of rooting by wild boars is the reduction in plant cover (Singer et al.,
1984; Massei & Genov, 2004). Surprisingly, ground gleaning birds in our study were not
statistically affected by wild boar foraging. This strongly support the idea that wild boar mediated
effects observed in this study resulted mainly from direct predation on birds and nests or increased
predation risk, rather than food competition. In a remarkable long-term study, Wesolowski et al.
(2009) showed that wood warblers abundance in Bialowieza forest was inversely correlated with
small mammal predator densities and were only weakly correlated with caterpillar abundance; the
nomadic behavior of wood warblers appears to be a consequence of their attempts to breed in safe
places. Although most studies focused on the direct negative effects of wild ungulates on habitat
alterations and invertebrate availability, large herbivores may affect many species of plants and
animals through indirect effects (Suominen & Danell, 2006; Barrios-Garcia & Ballari, 2012). Large
ungulates concentrations may have both positive and negative effects on insectivorous birds;
positive effect being probably mediated by nutrient input through the ecosystem (Mathisen & Skarpe, 2011; Mathisen et al., 2012). This type of complex interaction may explain the observation in our study, that tree foraging birds showed light increases in areas strongly foraged by wild boars. However, one should note that ground nesting birds (Bonelli’s warbler, that are also tree foraging birds) were subtracted from this guild. As a result, this guild of “tree foraging birds” consisted of only two species, which require a careful interpretation. Future research is thus needed to better understand these mechanisms or confirm this result.

As final words, none of the birds species observed in this study are listed as threatened species; however wild birds trends are commonly used as indicators of environmental health and biodiversity (Gregory & van Strien, 2010). As common bird species shape the ecosystems, even relatively small declines in their ranks can disrupt ecosystem structure (Gaston & Fuller, 2008); as a consequence, monitoring bird indicators may give understanding on other taxa. Numerous studies underlined the decline of common palearctic birds in Western Europe (Birdlife international, 2004; Gregory & van Strien, 2010; EBCC, 2015). Recently, Gregory et al. (2007) showed that birds nesting on the ground or in low vegetation declined more than those nesting higher up in shrubs and trees. Species trends at the European scale are thus more significantly correlated to nest-type (tree/shrub vs. ground/low vegetation) than to other ecological factors (migration, diet, region), a report that is true for both farmlands and forest birds. It is also suggested that predation may be an important factor influencing bird species trends in Europe (Fuller et al., 2007b; Gregory et al., 2007). Despite these reports, there are actually few managing programs that monitor the potential impacts of wild boar at large scales. As wild boar populations will continue to grow in Europe (Massei et al., 2015), the development and use of new impact indicators may be critical for future bird and environmental management.
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