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Comparing sampling methods to monitor population abundance while accounting for imperfect detection: an application of *N*-mixture models on Orthoptera

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Abstract

Human activities are profoundly altering natural ecosystems, impacting both the distribution and abundance of animal populations. Monitoring is the base for assessing the status and temporal changes in animal populations. Among the various considerations involved in establishing a monitoring program, the choice of sampling methods can significantly influence the project's outcomes. In this study, we compared two sampling methods to monitor Orthoptera communities: sweep netting and tube sampling (a modified version of box quadrats). Imperfect detection can strongly bias the outcome of statistical models. Therefore, to compare the two sampling methods, we performed *N*-mixture models to take into account detection probability and uncertainty in abundance estimates. Between June and September 2023, we sampled Orthoptera communities across 25 sites in northern Italy, including a broad variety of grasslands, which are ecosystems holding high ecological value in agricultural landscapes. We detected a total of 35 species, 33 through sweep netting and 30 through tube sampling. *N*-mixture models were performed on the 14 most abundant species detected with both sampling methods. While detection probability was similar between the two sampling methods, the precision of detection estimates was markedly higher when using sweep netting. Additionally, abundance estimates were generally higher and showed less uncertainty when using sweep netting instead of tube sampling. These results suggest that, in our study system, sweep netting seems to be the best method to monitor Orthoptera communities. Still, the limited area sampled with tube used here (2–4 m^2 per survey in each plot) possibly influenced the precision of abundance estimates, and larger tubes or boxes may provide more accurate measures. Our framework to compare sampling methods can be applied to a broad range of organisms. It can help in deciding which method is better to fulfill the aims of multi-season monitoring programs by conducting pilot surveys at a small set of sites.

Keywords: Detection probability; grasslands; hierarchical models; orthopterans; box quadrats; sweep netting

Introduction

Human activities are profoundly altering natural ecosystems, including species distribution and abundance (Butchart et al., 2010; Dirzo et al., 2014). For instance, in Europe, about one fifth of the species assessed by the International Union for the Conservation of Nature are threatened with extinction (Hochkirch et al., 2023). Agriculture is one of the main drivers of environmental change, with agricultural fields and pastures covering around 40% of global land surface (Foley et al., 2005). Therefore, favoring biodiversity in agricultural lands will be a key strategy to supplement protected areas and assist sustainable exploitation of natural resources (Kremen and Merenlender, 2018). Animals are key components of agroecosystems, often providing essential ecosystem services such as pollination, seed dispersal, or pest control (Egerer et al., 2018; Kremen et al., 2002; Shine et al., 2024), or disservices such as crop consumption or predation of beneficial taxa (Tschumi et al., 2018a, 2018b). It is therefore crucial to assess the status and trends of animal biodiversity in agroecosystems, in order to promote practices that can sustain both agricultural production and ecosystem services provided by animals (Kremen and Merenlender, 2018).

Natural and semi-natural grasslands hold high ecological values within European agroecosystems, being among the most species-rich habitats (Dengler et al., 2014). These environments can supply direct goods such as fodder for livestock, but can also provide other services such as pollination, pest control, carbon storage, or cultural services (Bengtsson et al., 2019). Insects are key components of grassland ecosystems, covering a broad range of roles, from herbivores to predators and pollinators. Among herbivores, Orthoptera are key components of the trophic chain in many grasslands (Buri et al., 2013). Orthoptera are mainly primary consumers, able to reach high densities in grassland environments, hence being of primary importance for energy transfer across trophic levels (Belovsky and Slade, 2018). Both local habitat characteristics and management can influence Orthoptera abundance and community composition (Weiss et al., 2013).

For instance, delayed cuts or leaving uncut areas as a refuge are two management practices that can benefit Orthoptera abundance and persistence (Humbert et al., 2012).

Monitoring animal populations is the basis for assessing biodiversity status and temporal changes. Imperfect detection is a pervasive issue in biological research and can strongly bias statistical inference (Kellner and Swihart, 2014). This means that the number of individuals counted during a survey at a site is usually lower than the true number of individuals present. This discrepancy will result in the underestimation of the population size and in biased estimates of relationships between environmental factors and abundance of the target species (Guillera-Arroita et al., 2014). It is therefore essential to adopt sampling designs able to incorporate detection probability in order to correct abundance estimates. This is usually achieved with repeated surveys within one or multiple sampling seasons (Pollock, 1982). Then, hierarchical statistical models, such as *N*-mixture (for abundance) or occupancy (for presence/absence) can be applied, allowing the estimation of detection probability and true abundance (Royle, 2004). In this context, the sampling method used can be crucial in determining the outcome of abundance estimates.

When establishing a monitoring program for a species, several choices have to be taken, including the number and location of study sites, the frequency of surveys, and the sampling method to be used. Sampling methods used can strongly influence the outcome of monitoring, therefore studies comparing different methodological choices can facilitate decision-making for planning population monitoring. Several sampling methods are available to monitor Orthoptera populations (Gardiner et al., 2005). In this study, in order to choose the best sampling method for a multi-year monitoring program, we performed monitoring of Orthoptera populations comparing two sampling methods: sweep netting and tube sampling (a modified version of box quadrats).

Despite its potential strong bias on statistical inference, explicitly considering imperfect detection is not the standard practice in studies comparing sampling methods (Costello and Daane, 1997; Gardiner and Hill, 2006; Merz et al., 2021; Monzo et al., 2015). Therefore, here we show how *N*-mixture models can be implemented to compare different sampling methods while jointly taking into account uncertainties in abundance estimates. Our process is applicable to a broad range of organisms. It can help in deciding which sampling method is better to fulfill the aims of multi-season monitoring programs, for instance by conducting pilot surveys at a small set of sites.

Materials and Methods

Study area and sampling

Between June and September 2023, we sampled 25 grasslands located in northern Italy, between Lombardy and Trentino Alto-Adige regions. In order to include a broad range of environments, study sites were located in two main areas (Fig. 1a). The first area includes 10 sites located at mid-elevation and in high mountain areas, between 970 m and 2,370 m a.s.l. within the Martello Valley. Study sites of Martello Valley included various habitats, from hay meadows to pastures (Fig. 1b). The second area includes 15 sites located within the metropolitan area of Milan, the main city of northern Italy. Study sites were evenly chosen across three urban parks (five per park): Bosco in Città, Parco delle Cave, and Parco Nord (Fig. 1c). Study sites in this area comprise both meadows repeatedly cut during the year and less disturbed grasslands cut once a year or every other year.

At each site, we performed six surveys within the study period, using two sampling methods: sweep netting, and tube sampling. Therefore, for each site, we collected data over six replicate occasions through sweep netting and six through tube sampling.

Sweep netting

The first sampling method used is the sweep netting along transects (Fig. 2a). This is one of the most used methods for sampling Orthoptera and other insects (Gardiner et al., 2005; Stoch and Genovesi, 2016), and its accuracy has been evaluated by Larson et al. (1999). The standard method consists of sweeping the vegetation with a net moving in an arc from left to right and back in front of the observer. To ensure total coverage a high number of sweeps is often used, usually dependent on the size of the study site. In our study, we standardized the number of sweeps using transects: the number of transects performed at each plot was based on the plot area and remained constant for each site along the sampling season. The number of sweep netting transects was chosen based on the number of transects required to cover the entire site area. To catch the Orthoptera, we performed 20 sweeps along each transect, maintaining a rate of ~1 sweep per meter. We used a net featuring a 60 cm handle, a metal ring of 40 cm diameter, and a green net 76 cm deep. At each survey in a site, we placed between 2 and 5 transects of 20 m length and ~1 m wide, disposed to occupy all the plot area.

Tube sampling

The second method used is similar to the box quadrats used by Gardiner and Hill (2006). We decided to use a modified version of the box quadrats, more convenient and portable, here referred to as "tube sampling". Instead of using a plastic and wooden box (Gardiner et al., 2005), we decided to use a compressible tube (hereafter, "box") with a diameter of 55 cm and 130 cm height (Fig. 2b, 2c). This solution is effective in temporarily confining Orthoptera but is much lighter and more portable compared to classic rigid boxes. To catch Orthoptera, the tube was quickly dropped onto the ground every 10 steps within the site area (Fig. 2b). The tube was firmly held on the ground to avoid the escape of any insect, while the operator checked the presence of orthopterans in the tube (Fig. 2c). The number of drops of the tube at each site was calculated as the number of sweep netting transects + 1 and then multiplied by three. Therefore, the number of tube drops could vary between nine (small sites with two sweep netting transects) to 18 (large sites with five sweep netting transects). The number of tube drops was chosen to have a sampling effort proportional to the site area and to the number of sweep netting transects performed. Moreover, preliminary surveys showed that after 15-20 tube drops per site no additional species were recorded.

At the end of each sweep netting transect or tube drop, all the captured Orthoptera were counted and identified at the lowest taxonomic level possible. In most cases, identification was performed directly in the field, still, when field identification was not possible, the specimen was collected in a 2 ml vial and prepared for identification under a stereomicroscope. Identification was made following identification keys from Fauna d'Italia (Massa et al., 2012), Grasshoppers of Italy (Iorio et al., 2019), and Grilli e cavallette del Veneto (Fontana et al., 2002).

Statistical analyses

Data collected through sweep netting and tube sampling were used to estimate the abundance of Orthoptera species at each study site. While we detected 35 species across the 25 study sites (Supplementary material, Tab. S1), we estimated abundance only for the 14 species for which we had at least 10 records over the study period.

For each species, we estimated abundance through *N*-mixture models, which are hierarchical models that take into account detection probability when estimating population abundance (Madsen and Royle, 2023). Being successfully applied to a wide range of taxa (Falaschi et al., 2022; Ramellini et al., 2024; van Strien et al., 2024), *N*-mixture models are considered a robust method to estimate population abundance based on replicated counts, without the need for marking individuals. In *N*-mixture models, the true abundance is a latent variable (N) that is estimated thanks to two sub-models: an ecological sub-model, describing abundance and environmental variables possibly related to abundance, and an observational model, estimating detection probability and its potential drivers. We defined the abundance sub-model as:

$$N_i \sim Poisson(\lambda_i)$$

meaning that we assumed the true abundance N to follow a Poisson distribution with mean λ, being i the site index. The detection sub-model was defined as:

$$y_{ij} \sim Binomial(N_i, p_{ij})$$

meaning that the observed count y followed a binomial distribution with size N and detection probability p, with i and j being the site and survey index respectively. Additionally, since the availability of orthopterans can be strongly seasonal, we used the day of the year as a covariate of detection probability to take into account phenology, as follows:

$$logit(p_{ij}) \sim \alpha + \beta \times day_{ij}$$

here α is the intercept, β the regression coefficient, and day_{ij} the day of the year of survey j at site i.

We implemented our models in a Bayesian framework using nimble (de Valpine et al., 2017) and calculated a derived parameter indicating the total abundance of each species across the study area, as follows:

$$N_{tot} = \sum_{i=1}^{nsite} N_i$$

with $nsite$ being the total number of sites. To avoid an artefactual inflation of total abundance estimates, for each species we excluded the sites that were outside the known species' range (see Table S1 for a complete list of the sites used for each species).

Analyses were performed in the R environment (version 4.2.3), using the "nimble" package (de Valpine et al., 2017; NIMBLE Development Team, 2023). Priors of α and β followed a normal distribution with mean = 0 and precision = 0.01, while the prior of λ followed a uniform distribution bounded between 0 and 1000. For each model, we run three Markov Chains Monte Carlo, for a total of 40,000 iterations each. The first 30,000 iterations were discarded as a burn-in and the posterior distributions were sampled with a thinning of 10, obtaining 3,000 posteriors (1,000 for each chain). Parameters convergence was inspected visually and by looking at Rhat values.

Comparing methods

A good sampling method should be efficient in detecting individuals; therefore, a high detection probability is preferable. On the other side, when estimating abundance, we want to approach the true population size, with the smallest uncertainty possible; hence, a method showing higher precision in abundance and detection estimates is preferable. Consequently, to compare the performance of sweep netting and tube sampling, we looked at species-specific detection probabilities and abundance and, additionally, at the standard deviations of detection probability and abundance.

Results

Overall, we found 35 species across the 25 study sites. Study sites in the Martello Valley (Fig. 1b) hosted 15 species and study sites in Milan area (Fig. 1c) hosted 22 species, with only 2 species being shared by the two areas. A total of 2,295 captures belonging to 33 species were made through sweep netting, while tube sampling returned 981 captures from 30 species (Fig. 3). The number of detected species per site was on average 5.3 with sweep netting (range: 1–12) and 5.0 with tube sampling (range 1–11). All abundance models reached convergence both for sweep netting and tube sampling, with Rhat values <1.1 for all parameters (Table S2).

Sampling methods comparison

Median detection probability varied between <0.001 for *Chorthippus* spp. using tube sampling and 0.43 for *Gomphocerus sibiricus* with tube sampling (Table S2). On average, detection probability using tube sampling was slightly higher than detection probability using sweep netting (average detection probability across all species 0.238 for sweep netting, 0.247 for tube sampling), still, there was large variability across species (Fig. 4). Some species showed higher detection probabilities with one method (e.g., *Chorthippus brunneus* and *Euchorthippus declivus* using sweep netting, *Podisma pedestris* using tube sampling; Table S2), still, for most of the species we did not detect large differences (Fig. 5a).

Total abundance across sites (Fig. 4), varied from 5 (95% Credible Interval [CI] = 5–10) for *Oedipoda caerulescens* using tube sampling, to 375 (95% CI = 311–483) for *Omocestus rufipes* using sweep netting (Fig. 4). Overall, sweep netting returned higher abundance, with 13 out of 14 species showing median abundance estimates higher or equal than tube sampling (Fig. 5b).

When looking at the standard deviations of detection probability estimates, for most species (12 out of 14) sweep netting returned lower standard deviations, indicating a higher precision compared to tube sampling (Fig. 5c). The picture was similar for the standard deviations of abundance estimates, where the majority of the species (9 out of 14) showed higher precisions when using sweep netting (Fig. 5d).

Discussion

By applying *N*-mixture models to Orthoptera counts, we showed how it is possible to compare two sampling methods while accounting for uncertainty due to imperfect detection. Our results showed that while detection probabilities were overall similar between the two methods, sweep netting returned more precise estimates of detection probabilities compared to tube sampling (lower standard deviation of detection probability for 86% of species; Fig. 5). Additionally, abundance estimates were generally larger for sweep netting (93% of species) and also more precise in 64% of species, indicating that sweep netting likely returns estimates closer to the true densities at study sites. In our case study, sweep netting seems to be the best choice for monitoring Orthoptera communities, considering that sweep netting also detected more species and individuals (2,295 individuals from 33 species sweep netting; 891 individuals from 30 species tube sampling).

It is also important to point out that the best sampling method can be species-specific. Looking at our results, while sweep netting seems to be the best choice for most species, in some cases tube sampling may be better. For instance, estimates of the detection probability of *Podisma pedestris* were markedly higher with tube sampling (Fig. 4). *Podisma pedestris* is a species that exploits alpine grasslands and pastures with low vegetation and presence of shrubs such as juniper (*Juniperus* sp.). The species is flightless and usually moves on the ground, resulting in a lower efficiency of sweep netting compared to tube sampling. In other cases, sweep netting was largely the best choice for sampling some species, such as for *Chorthippus brunneus*, showing both higher and more precise detection and abundance estimates with sweep netting compared to tube sampling (Fig. 4). Another example is *Aiolopus thalassinus* for which sweep netting showed higher detection probability estimates. Abundance estimates for this species showed similar average values, still, the error showed by tube sampling was markedly larger compared to sweep netting (Fig. 4). Both these species (*C. brunneus* and *A. thalassinus*) are good fliers that frequently move from plant to plant, hence, they are easily captured using nets. The best sampling method may also be habitat-specific. For instance, while sampling, we observed that in the presence of woody vegetation or irregular soil (e.g., presence of rocks or twigs), the tube used in tube sampling cannot be firmly held onto the ground. As a consequence, Orthoptera can easily escape passing below the tube, hampering the efficiency of tube sampling in some environments.

Previous studies already compared several sampling methods to monitor Orthoptera (Gardiner et al., 2005; Gardiner and Hill, 2006). For instance, Gardiner and Hill (2006) compared three sampling methods, suggesting that methods that temporarily confine individuals to avoid movement outside sampling plots return better density estimates. Still, these studies did not take into account imperfect detection, which can severely bias estimates of abundance (Kéry and Royle, 2021). Accounting for detection probability and uncertainty in abundance estimates can add relevant information. For instance, we showed that abundance estimates are not only higher but generally more precise using sweep netting compared to tube sampling (Fig. 5). This means that the best method is not always the one returning the highest counts, since also uncertainty is relevant for conservation purposes (Johnson et al., 2024).

The low precision of our version of the box quadrat method (i.e., tube sampling) is somehow surprising considering the broad application of box quadrats in Orthoptera research and monitoring schemes (Fartmann et al., 2022; Gardiner et al., 2005; Gardiner and Hill, 2006; Streitberger et al., 2024). Fartmann et al. (2024) showed that the box quadrat method returns very accurate measures of species richness and abundance, suggesting sampling an area of 20 m^2 for each site. Our tube sampling method involved the usage of a tube of 55 cm diameter, which covers an area of ~0.24 m^2. At each site, we performed from a minimum of nine to a maximum of 18 tube drops, hence covering an area between 2.1 and 4.3 m^2 at each survey at a site. Given that at each site we performed six surveys, the total area covered across the entire sampling season is much higher, in the range of 13–25 m^2 per site. Since *N*-mixture models use single surveys as separate data points, the low accuracy of tube sampling might be determined by the small area covered during each survey. Still, when comparing densities obtained through tube sampling with densities obtained through box quadrats by Fartmann et al. (2024), we generally obtained higher density estimates for 8 of the 9 species in common between the two studies (Figure S1). Therefore, we stress that our results do not indicate a low accuracy of the box quadrat or tube sampling methods in general but only refer to performing *N*-mixture models with tube sampling data.

Multi-season monitoring programs are essential to assess biodiversity changes and to plan conservation actions. The choice of the most appropriate sampling method is crucial for retrieving information for sound evidence-based conservation. Here we showed how *N*-mixture models can be applied to a handful of sites to make informed decisions. Ideally, multi-season monitoring programs can devote the first season of monitoring to the choice of the most appropriate sampling method. During this first season, two or more alternative sampling methods can be tested on a subset of sites, then, analyses of data from the first season can drive the decision of the best-suited method based on the aims of the monitoring (e.g., target species or habitat). Given that conservation biology is always a matter of choice, making informed decisions is of primary importance (Schwartz et al., 2018; Sutherland et al., 2004).

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Data availability statement

All data used in this work are available at Figshare, along with the scripts used to run abundance models: https://figshare.com/s/532a9c61fa3a83391a1b

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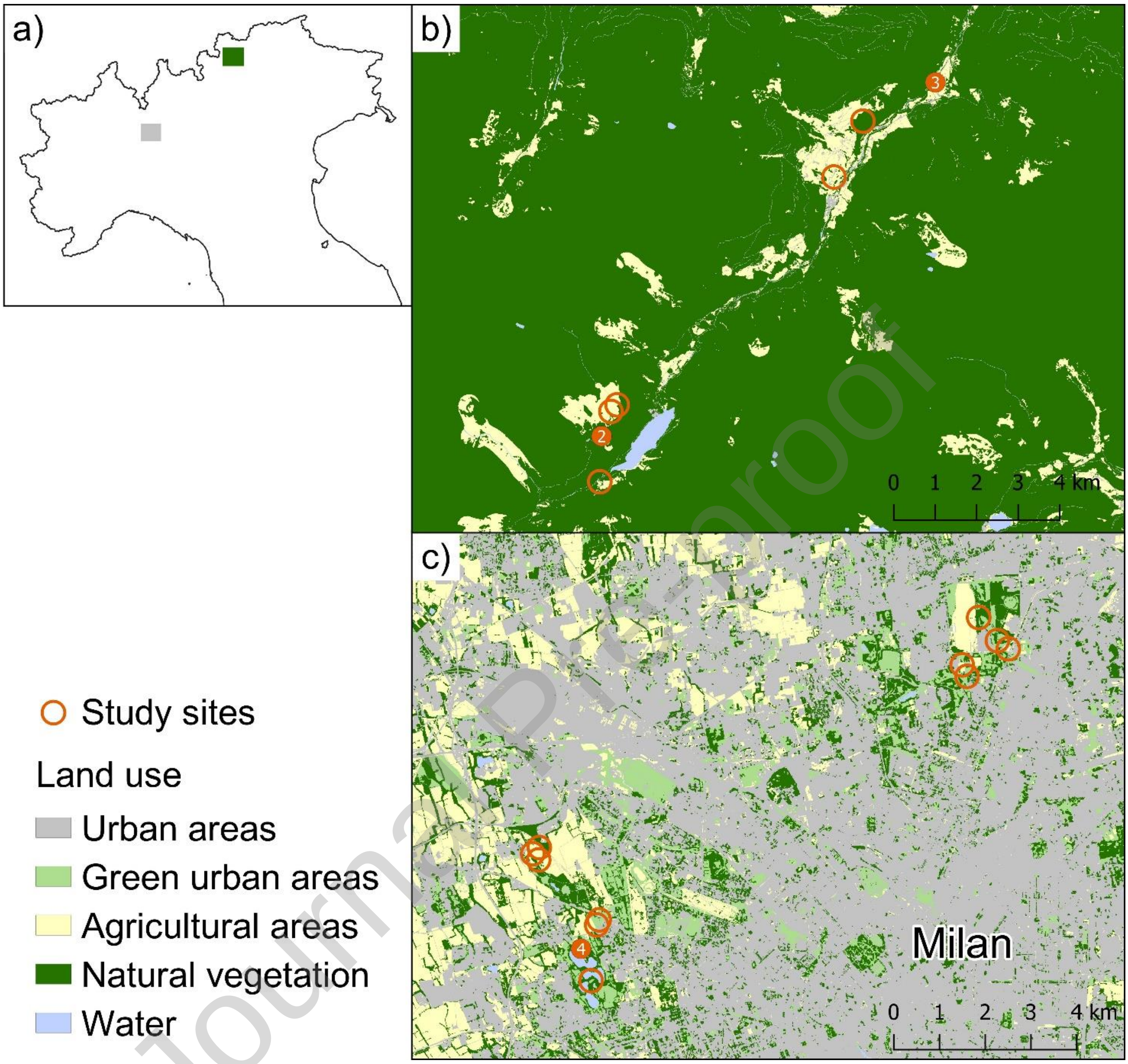

Fig. 1. Study area. Location of the 25 study sites in northern Italy (a), and more detailed maps of study sites within the Martello Valley (b) and around Milan (c). The numbers within closed orange circles in b and c indicate the number of sites that are overlapping at this scale. Martello Valley is indicated with a green rectangle in "a", and the Milan area is in grey. Base map derived from Marsoner et al. (2023).

Fig. 2. The two sampling methods compared: sweep netting and tube sampling. The first author (AMD) performing monitoring of Orthoptera populations with sweep netting (a) and tube sampling (b, c).

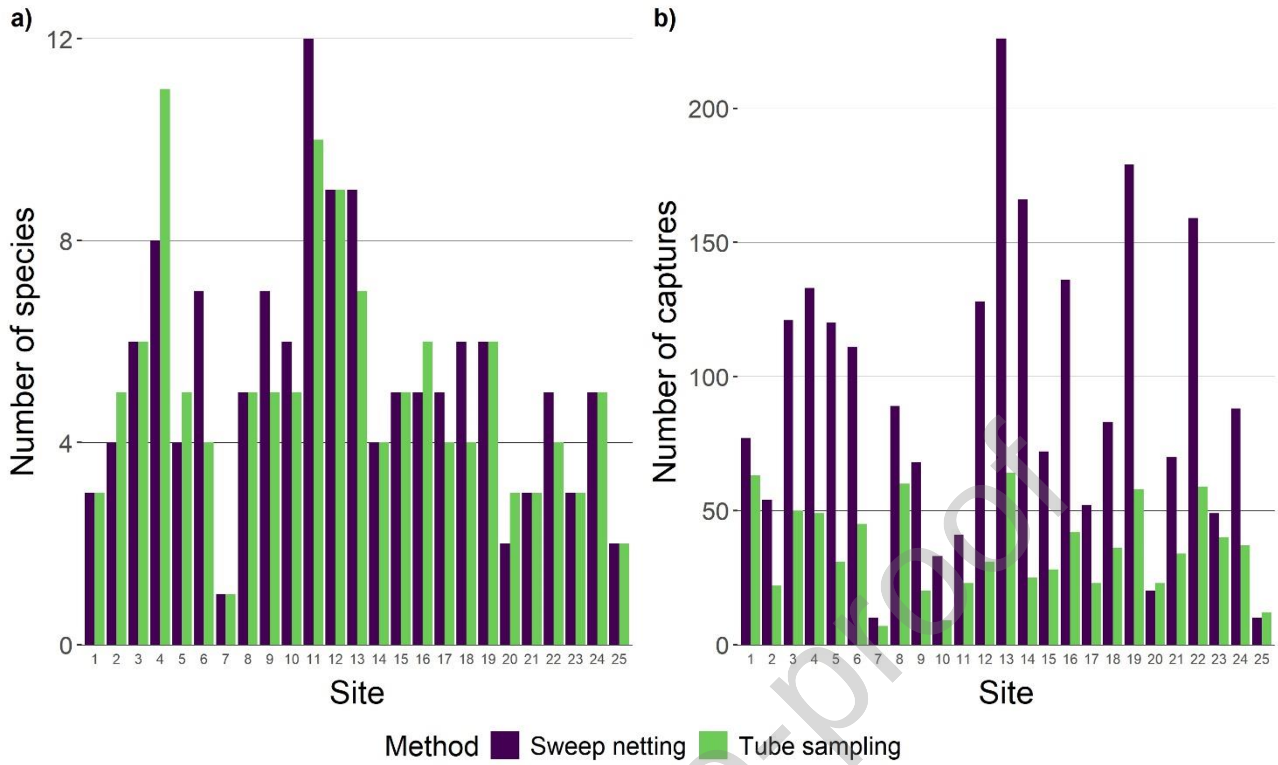

Fig. 3. Number of species and number of captures obtained at each site with the sampling methods. For each site, the number of species (a) and number of captures (b) performed with the sweep netting and tube sampling are shown. Dark purple: sweep netting; green: tube sampling.

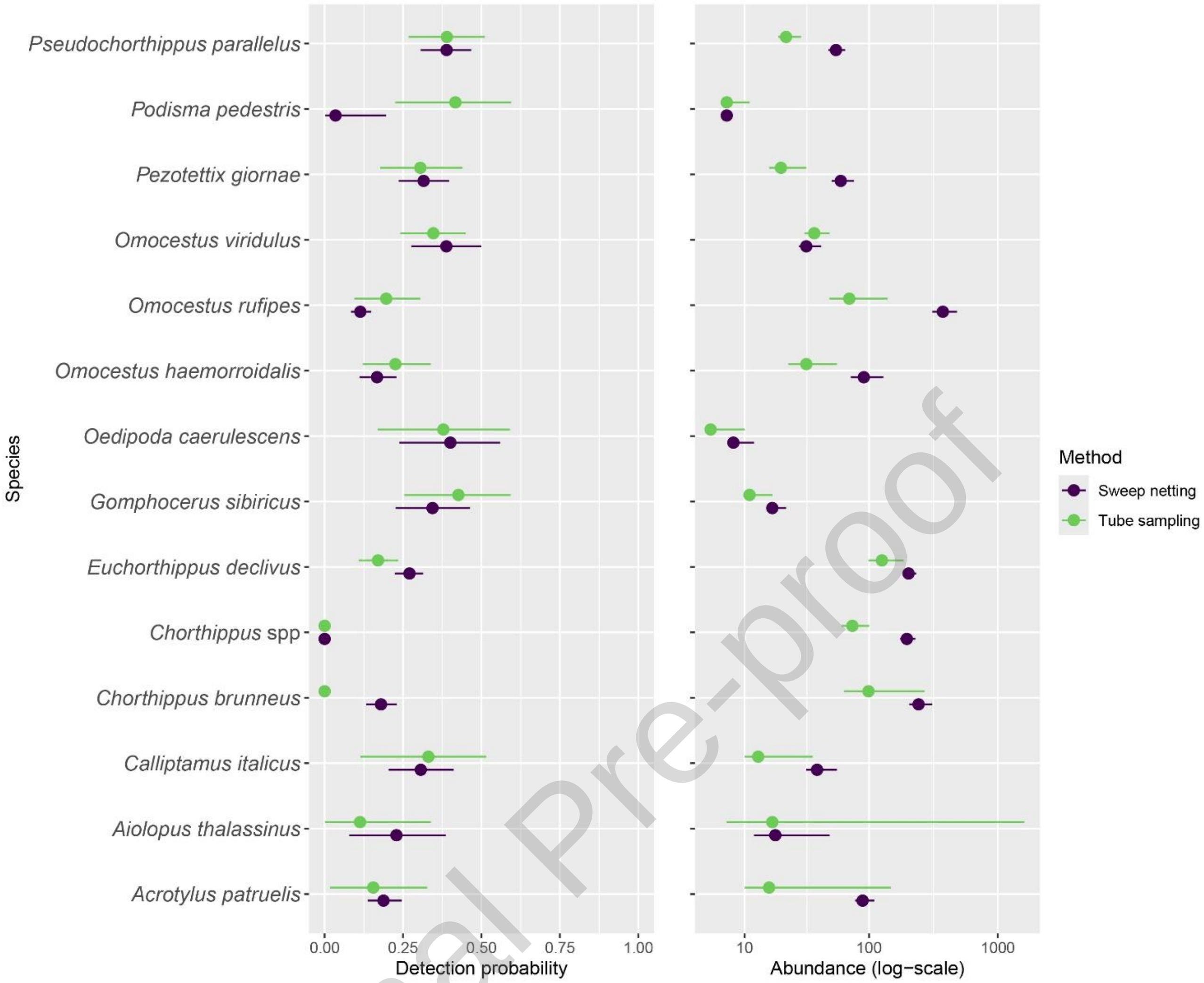

Fig. 4. Detection probability and abundance estimates for 14 orthoptera species. For each species, estimates of detection probability (left) and abundance (right, log-scale), are shown for the two sampling methods. Dark purple: sweep netting; green: tube sampling.

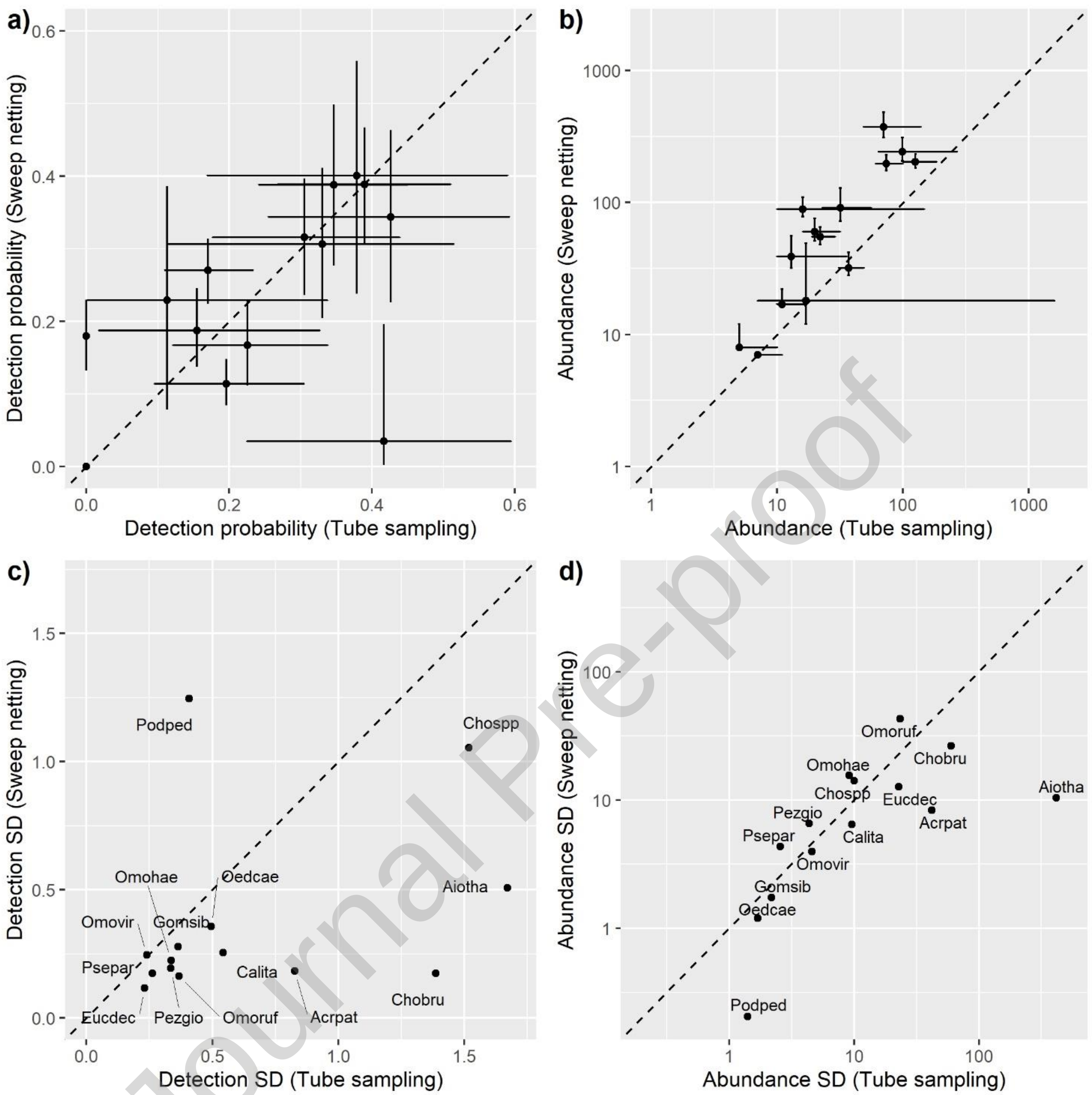

Fig. 5. Comparison of estimates and standard deviations of detection probability and abundance. For each species, we show detection probability (a) and abundance (b) estimates, along with 95% Credible Intervals and standard deviation for detection probability (c) and abundance (d). Values for tube sampling are on the horizontal axes, while values for sweep netting are on the vertical axes. Dashed lines represent the 1:1 ratio, indicating equal values for the two sampling methods. Species names are abbreviated as the first three letters of the genus and the specific epithet in c and d. Complete species names are available in Fig. 3.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Ethics Statement

Handling of live Orthoptera was performed in order to minimize the manipulation time. Individuals were hold by the thorax to avoid autotomy of legs. Only specimens for which identification in the field was not possible were collected. No protected or endangered species were collected.