Cricket calling communities as an indicator of the invasive ant Wasmannia auropunctata in an insular biodiversity hotspot

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Abstract Invasive species are a major concern for the maintenance of ecosystem services and biodiversity but are difficult to mitigate. Upstream solutions to prevent their impact, including their detection, are needed. *Wasmannia auropunctata*, an invasive ant living in vagile supercolonies, is especially hard to track and is a major threat for tropical ecosystems and local animal communities. As part of such tropical communities, crickets are sensitive to ecological conditions, easy to collect, detectable and identifiable through their species-specific calls. Here, we evaluated the use of an acoustic community of crickets as an indicator of the presence of *W. auropunctata* in New Caledonia. We evaluated the dominance of the crickets in the soundscape, describe the cricket community structure and diversity along a shrubland to forest gradient, characterize these cricket communities structure and diversity in the light of ongoing invasion by *W. auropunctata*, and identify cricket species' indicators of the invasion. Acoustic recordings collected on 24 sites were described using human-listening and spectrographic visualization. The results demonstrated a clear dominance of the cricket group in the New Caledonian nocturnal soundscapes. Each habitat harbored a specific acoustic cricket community related to specific environmental attributes including vegetation height, daily variation of humidity and temperature. The presence of *W. auropunctata* was significantly associated with a lower cricket acoustic activity and species richness at night. Of the 19 species detected, four nocturnal species were identified as indicator of non-invaded forests and preforests. This work supports the use of acoustic as an alternative method to detect invasion.

Keywords Bioindicator · Acoustic community · Invasive species · Soundscape · Ecoacoustics

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Introduction

Biological invasion is one of the major drivers of ongoing global environmental change (Vitousek et al. 1996; Simberloff et al. 2013). Because negative impacts of invasive alien species on ecosystem services, community structure, and biodiversity are important and difficult to mitigate, upstream solutions to prevent impact of invasive species are needed (Hulme 2006; Ehrenfeld 2010; Simberloff et al. 2013). Among invasive species, ants receive specific attention due to their demonstrated association with ecosystem function and biodiversity loss (Lach and Hooper-Bui 2010). Invasion success of this group resides in their low intra-species aggression (unicoloniality), high inter-species aggression, mutualism behavior, and high competition for local resources with native species (Holway 1998; Holway et al. 2002). Environmental managers need efficient tools to detect their presence, evaluate their impacts, and track their spread to initiate management action as early as possible (Hulme 2006). In this context, invasive ants that are small and live in mobile colonies are especially hard to track.

Recent advances in ecoacoustics contributed to the idea of using sound from the activity of an animal community as an indicator of environmental conditions or ecological changes (Pijanowski et al. 2011; Sueur and Farina 2015). In both terrestrial and aquatic environments, many animal species rely on acoustic signals to interact. Species acoustically active in a given space and at a specific time constitute an acoustic community contributing to the soundscape. The term soundscape here is defined as the "physical extent of acoustic signals and the spectral range of signal frequencies associated with an ecosystem's biophysical processes" following Qi et al. (2008). Acoustics of animal communities can reflect their diversity, composition and dynamics and be indicative of environmental trends (Gasc et al. 2013; Lellouch et al. 2014; Towsey et al. 2014). Several studies have linked the acoustic profile of animal communities with habitat characteristics and/or human disturbances (Sueur et al. 2008; Joo et al. 2011; Tucker et al. 2014). Based on these promising results, the direct influence of biological invasion on acoustic communities in the natural environment needs to be investigated (Boelman et al. 2007).

Among soniferous insects, crickets (Orthoptera, Grylloidea) possess several of the required qualities to potentially be bioacoustic indicators in the tropics: (1) crickets are widely distributed in the tropics with reasonably high overall abundance and wide local diversity (Otte and Alexander 1983; Otte 1994; Desutter-Grandcolas et al. 2016), (2) many cricket species rely on acoustic signals to attract a mate, and their calls are most often species-specific and easy to identify (Riede 1997; Diwakar and Balakrishnan 2007), (3) convincing evidence placed crickets as sensitive to environmental changes, including ecological succession (Desutter-Grandcolas 1992; Szinwelski et al. 2012) and biological invasion (LaPolla et al. 2000). In this context, the survey of the acoustic community of crickets could represent a fast and efficient approach for habitat surveys in general and for the detection of invasive species in particular.

To test this hypothesis, we conducted an acoustic survey of the abundant, diverse and well-described cricket communities in New Caledonia (Anso 2016; Anso et al. 2016b). New Caledonia is a Pacific archipelago, considered a major biodiversity hotspot that is threatened by human activity and invasive species (Myers et al. 2000). Among invasive ants, *Wasmannia auropunctata* (Roger 1863) appears as one of the "six most widespread, abundant, and damaging invasive ants" in the world (Holway et al. 2002) and one of the "100 world's worst invasive species" (Lowe et al. 2000). This species spreads and impacts biodiversity in all New Caledonian habitats (Jourdan et al. 2001; Le Breton et al. 2003; Berman et al. 2013). For this survey, we selected 24 sites in the south of the main island according to two critical ecological conditions: the habitat type and the presence *W. auropunctata*. We passively recorded and analyzed soundscapes from these sites to evaluate the dominance of the cricket group in the overall acoustic community, described the structure and diversity of the calling cricket communities in three dominant habitats, and characterized the response of cricket calling communities to the ongoing invasion by *W. auropunctata* on the cricket calling communities.

Methods

Study sites

Selected sites were on similar metalliferous soil in southern New Caledonia, hosting three main habitat types following a vegetation gradient: "forest", "pre-forest" and "shrubland" (Online Resource 1). We selected invaded and non-invaded sites leading to a total of six modalities (3 habitat types × 2 invasion conditions). Each modality was replicated four times for a total of 24 sites (Online Resource 2). Sites were reported as invaded and non-invaded by researchers of the Institute of Research and Development of Noumea. To characterize the invasion by *W. auropunctata* on these sites, we established two perpendicular transects of 200 m oriented North–South and East–West in each site, centered on the acoustic sensor. We investigated the presence/absence of *W. auropunctata* during 5 min at the sensor location and at 50 m and 100 m from the recorder along the transects. 'Non-invaded' sites were associated with more than 85% of the check-points free of the invasive, and 'invaded' sites were associated with more than 85% check-points where the invasive was found. This evaluation was conducted just before the acoustic sampling. All sites were at 189 m (SD 83) elevation above sea level and separated by at least 200 m.

Acoustic recording procedure

We collected recordings during the dry season, from 17 October to 26 December 2013 with automatic field recorders, SongMeter SM2 and SM2 + (Wildlife Acoustics, Concord, NY, U.S.A.), that have similar technical specifications for each modality (Online Resource 2). We deployed one recorder on each site. We equipped each acoustic sensor with two omnidirectional microphones (frequency response: − 35 Decibels (SD 4) between 20 Hertz and 20,000 Hertz) oriented horizontally, one at 1.5 m and the other at 30 cm from the ground. We set the gain to + 36 Decibels and the sampling frequency rate at 48,000 Hertz (16 bits). We configured the acoustic sensors to record 2 min every 58 min. We first stored the files in the lossless compression format.*wac* and then transformed them into.*wav* with the software Kaleidoscope version 1.1.20. The files were examined (n = 20,512)

to discard those (n = 3 056) containing anthropogenic noise (e.g. human voices), rain and/or wind.

Calling identification and count

For each site, we selected 120 recordings, corresponding to the beginning of every hour—from 07:00 to 16:00 h and from 19:00 to 04:00 h—for 6 days randomly selected. We deliberately discarded dusk and dawn choruses, at 05:00 and 06:00 h and at 17:00 and 18:00 h, because of the dominance of overlapping bird sounds. We simultaneously listened and visualized the selected recordings using a spectrogram generated with Audacity (non-overlapping 1024 sample Blackman-Harris window), for a more accurate discrimination of call overlaps (Truskinger et al. 2013). First, we classified calls—defined here as a distinct acoustic production—in four main acoustic groups as follow: birds, crickets, katydids and others (cicadas, anurans, cats and bats). Then, we identified the cricket calls at a species level and counted the number of calls per species (Online Resource 3), based on taxonomic and acoustic descriptions published by Anso et al. (2016b).

Environmental variables

At each site, we delimited a plot of 10 square meters where we characterized the vegetation and the climatic attributes. We assessed bare ground and vegetation layers (herbaceous, shrubs, canopy) visually from the center of each plot. We counted trunks with a diameter at breast height (dbh) above 30 cm and assessed plant species richness by sight with help from a local botanist. We assessed canopy closure in the middle and four corners of each plot by evaluating the percentage of light in the forest over story with a 180° hemispherical lens and the Gap Light Analyzer software 2.0 (Frazer et al. 1999). We recorded climatic attributes including daily temperature (in °C) and relative humidity (in %) every 5 min using a waterproof thermo-hygrometer sensor (HOBO U23 Pro v2) attached to a tree (0.7 m) near the acoustic sensors. Daily variations in humidity and temperature corresponded to the difference between highest and lowest value for each parameter for each day.

Analyses

Analyses performed on the entire day (defined as all hours except the two chorus periods) are referred as '24-h' analyses. Analyses that focused on two time periods of the day, from 07:00 to 16:00 h and from 19:00 to 04:00 h, are respectively referred as 'daytime' and 'nighttime' analyses.

Non-invaded sites

To evaluate the dominance of the crickets in the New Caledonian soundscape, we calculated the percentage of occurrence—defined here as the total number of calls counted through the entire set of recordings—for each taxonomic group (crickets, katydids, birds and others) in the three selected habitats. This calculation was done separately for daytime and nighttime periods.

To assess the efficiency of the recording effort to describe the calling cricket community, we computed a species richness accumulation curve, which is the cumulative number of aurally identified species as a function of the cumulative recording number. As cricket communities are expected to vary depending on environmental conditions, we computed one curve for each habitat and for both 'daytime' and 'nighttime' periods. We computed these curves by considering the average value of species richness—values averaged among the four sites corresponding to the replication of the same habitat type. We followed the sample-based rarefaction method (Chiarucci et al. 2008). These curves were obtained with the function 'specaccum' available in the R package vegan version 2.2-1 (Oksanen et al. 2013).

To investigate the differences in cricket calling community structure between the types of habitat, and to investigate the possible relationship between environmental variables and the specificity of cricket community for each habitat, we performed a Non-metric Multidimensional Scaling (NMDS) with Bray–Curtis distances (Minchin 1987; Legendre and Legendre 2012). First, we calculated the distance between sampling sites based on the presence/absence data of cricket species identified from the 24-h period recordings (Minchin 1987). As recommended by Baselga (2008) to interpret the results, we set the stress value of the NMDS to 0.1 (random iteration = 1000, dimension = 2). Then, sampling sites were plotted together

according to habitat type. Environmental variables were fitted into ordination, and correlated with the species matrix with permutation test (random iteration = 999, $p < 0.05$). We performed an analysis of similarities (ANOSIM) to test for significant differences in community composition with habitat type as explaining factor, also using a permutation test (type I error rate at 5%). NMDS was performed using the function 'metaMDS' from the R package vegan (Oksanen et al. 2013). Environmental variables were fitted into ordination using the 'envfit' function from the same package.

Non-invaded and invaded sites

To evaluate the effect of *W. auropunctata* on the acoustic diversity of the cricket communities, we calculated the species richness (number of species identified) and the total number of calls counted by listening for each recording. Then, we computed a Generalized Linear Mixed Model (GLMM; Bolker et al. 2009) including the independent variables 'invasion' and 'habitat', considered as fixed effects, and the independent variables 'site', 'time', and 'date' considered as random effects (random intercept). The dependent variable was species richness for the model 1 and number of calls for the model 2, both fitted with a Poisson distribution with a log link function adapted for count data (Bolker et al. 2009). We ran these models separately on data collected during the nighttime and daytime periods using the function 'glmer' from the R packages lme4 (Bates et al. 2015). Validation steps for the models were not sufficient for the daytime data, but were sufficient for the nighttime period (Online Resource 4). Consequently, we only interpreted the results of the nighttime models. For both models, we obtained the p values of the effect of 'invasion' factor on, respectively, the number of species and the number of calls, by computing likelihood ratio tests of the full model and the model without the fixed effect 'invasion' (Bolker et al. 2009; type I error rate at 5%). As proposed by Nakagawa and Schielzeth (2013), we computed the marginal and conditional R^2 following the method adapted for GLMM with Poisson errors with Log link function.

To evaluate if the cricket community composition is singular under the invasion, we performed NMDS and ANOSIM analyses following the procedure

previously described. We conducted these analyses considering first the presence/absence of the cricket species and then the abundance of calls per species from non-invaded and invaded sites during 24 h. We excluded one invaded shrubland site from these analyses because of the absence of any species in the community and was therefore treated as an outlier in the analysis. The test of similarities ANOSIM were performed within each habitat, with the invasion as explanatory factor.

To identify species indicating the presence of *W. auropunctata*, we conducted indicator species analysis for each habitat independently and during 24 h (Dufrêne and Legendre 1997; De Cáceres et al. 2010). We calculated the non-equalized indicator species values and evaluated its significance by applying a permutation test (n = 1000 permutations; type I error rate at 5%) as suggested by De Cáceres and Legendre (2009) (similar results are observed with equalized indicator species values). We ran two sets of analyses separately, first using the presence/absence of the cricket species and then second using the abundance of calls per cricket species. Indicator species analyses were performed using the function 'mutli-patt' from the R package indicspecies (De Cáceres and Legendre 2009).

Results

Overall, the occurrence of species acoustically detected through 24-h analysis among the three habitats placed crickets as the dominant acoustic group (59.5%). Birds were the second acoustic group (31%), followed by katydids (7.9%). Different patterns of dominance between daytime and nighttime could be identified (Fig. 1). During the day, birds were the main acoustic group (58.8%), followed by crickets (34.1%) and katydids (5.6%). Considering the three habitat types, occurrence of cricket calls during the daytime accounted for 40.5% in 'forest', 25% in 'preforest' and 37.2% in 'shrubland'. Nocturnal cricket species largely dominated the nighttime soundscapes (85%), followed by katydids (10.1%) and birds (3.3%). Considering the three habitat types, occurrence of cricket calls during the nighttime accounted for 85.2% in 'forest', 73.4% in 'preforest' and 96.4% in 'shrubland'.
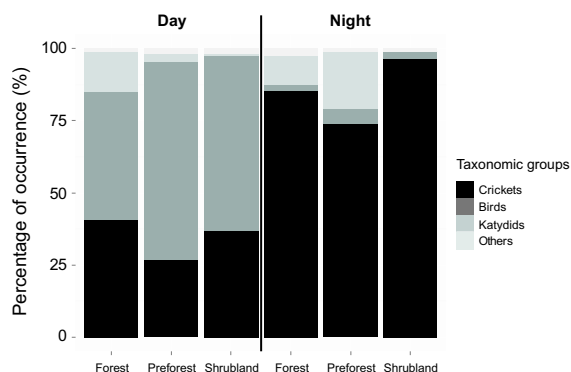

Fig. 1 Percentage of occurrence of calls in audio recordings for each acoustic group. The sample size for each habitat and time period is of 240 recordings

Species accumulation curves reached an asymptote over the period analyzed around three days of recordings, suggesting that acoustic communities have been almost completely sampled (Fig. 2). Considering the nighttime period, 'preforest' held the highest species richness with 10 species, followed by 'forest' with nine species, and 'shrubland' with five species. For the daytime period, the species accumulation curves followed the same pattern as during the nighttime period: 'preforest' held the highest species accumulation of acoustic species (six species), followed by 'forest' (five species) and 'shrubland' (three species).

From the recordings, a total of 19 cricket species were identified belonging to four families as defined by Chintauan-Marquier et al. (2016), i.e. Mogoplistidae with four species, Trigonidiidae with six species, Phalangopsidae with one species and Gryllidae with eight species. Among these 19 species, 10 were identified during daytime, and 16 during nighttime recordings (Table 1). Five out of 12 species were exclusively found in the forest, three out of 13 species in the preforest and one out of five species in the shrubland. Forest and preforest shared six species, preforest and shrubland shared three, and only one species, *Calcirtus magnus*, was found in the three habitats (Table 1).

NMDS ordination in two dimensions showed a clear effect of habitat type on acoustic communities (Fig. 3). Each habitat was fully discriminated with no overlap and supported by robust analysis of similarities (ANOSIM R^2 0.94, $p < 0.001$). The ordination was significantly explained by 12 environmental and bioclimatic variables that are: herbaceous layer, tree

Fig. 2 Species accumulation curves for cricket species in forest, preforest and shrubland. Gray areas indicate standard deviation
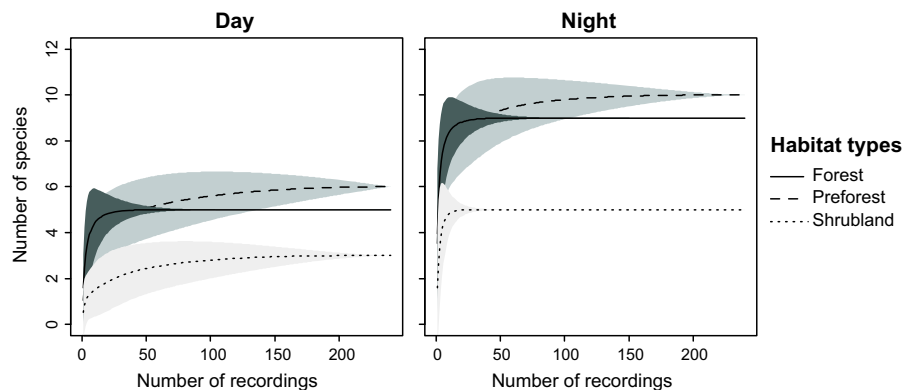

Table 1 Information related to species identified in the recordings with calling sites inferred from microhabitat of the species described. Reproduced with permission from Anso et al. (2016b)

Family	Species	Habitat	Diel calling	Calling sites
Gryllidae	*Agnotecous meridionalis*[a,d]	Forest	Night	Leaf litter
Gryllidae	*Agnotecous azurensis*	Forest/preforest	Day/Night	Leaf litter
Gryllidae	*Agnotecous clarus*[d]	Forest/preforest	Night	Leaf litter
Gryllidae	*Archenopterus bouensis*	Forest/preforest	Night	Canopy
Gryllidae	*Calscirtus magnus*	Forest/preforest/shrubland	Night	Canopy
Gryllidae	*Notosciobia affinis paranola*	Forest/preforest	Day/Night	Leaf litter
Gryllidae	*Notosciobia minoris*[e]	Forest/preforest	Night	Leaf litter
Gryllidae	*Notosciobia* sp1[b,d]	Preforest	Night	Leaf litter
Trigonidiidae	*Bullita fusca*[d]	Forest/preforest	Day	Leaf litter
Trigonidiidae	*Bullita mouirangensis*[a,d]	Forest	Day	Leaf litter
Trigonidiidae	*Bullita obscura*[b,d]	Preforest	Day/Night	Leaf litter
Trigonidiidae	*Koghiella flammea*	Preforest/Shrubland	Day/Night	Leaf litter
Trigonidiidae	*Koghiella nigris*[a]	Forest	Day/Night	Bare soil
Trigonidiidae	Trigonidiinae sp[b]	Preforest	Day	Understory
Mogoplistidae	*Mogoplistidae* sp1	Preforest/Shrubland	Night	Low veg.
Mogoplistidae	*Mogoplistidae* sp2	Preforest/Shrubland	Day/Night	Low veg.
Mogoplistidae	*Mogoplistidae* sp3[c,d]	Shrubland	Day/Night	Leaf litter
Mogoplistidae	*Mogoplistidae* sp7[a]	Forest	Night	Low veg.
Phalangopsidae	*Pseudotrigonidium caledonica*[a,d]	Forest	Night	Understory

"veg." calls for vegetation

[a] Species unique to forest

[b] Species unique to preforest

[c] Species unique to maquis

[d] Species absent in invaded area

[e] Species only present in invaded area

layer, bare ground, vegetation height, stem diameter, canopy closure, mean temperature, high temperature, daily temperature variation, mean humidity, lowest humidity, and daily humidity variation.

A total of eight species recorded in non-invaded habitats were absent in invaded areas (*Pseudotrigonidium caledonica*, *Agnotecous meridionalis*, *A. clarus*, *Bullita mouirangensis*, *B. obscura*, *Mogoplistidae* sp3
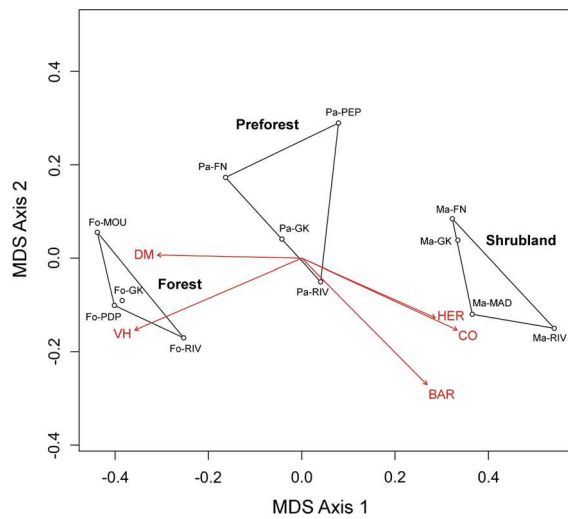
Fig. 3 NMDS (stress = 0.04, two dimensions) based on presence and absence of cricket species based on call identifications and environmental parameters. Twelve significant environmental variables are shown (ENVFIT, p < 0.05 with 999 permutations). Points represent the sites (n = 4 replicates per habitat type) and each of their site ID for the survey. Polygons were drawn according to habitat type. Sites, such as FO-PDP, are labeled according to the habitat type (FO for forest, PA for preforest and MA for shrubland) and then according to the locality name (see Table S1 for additional information). Abbreviations: 'HER' for 'Herbaceous layer', 'TRE' for 'Tree layer', 'BAR' for 'Bare ground', 'VH' for 'Vegetation height', 'DM' for 'DBH of stems', 'CO' for Canopy openness, 'MT' for 'Mean temperature', 'HT' for Highest temperature, 'DT' for Daily temperature variation, 'MH' for Mean humidity, 'LH' for Lowest humidity, 'DH' for Daily humidity variation

and *Notosciobia* sp1). By contrast, one species, *Notosciobia minoris*, was only recorded in invaded habitats (Table 1). A total of eight species were recorded in both invaded and non-invaded habitats: *Agnotecous azurensis*, *Koghiella flammea*, *K. nigris*, Trigonidiinae sp, *Mogoplistidae* sp1, *Mogoplistidae* sp2, *Notosciobia affinis paranola*, of which all were associated with a lower number of calls in presence of *W. auropunctata* (reduction of 76.17% (SD 19.81) of total calls observed per species) and *Mogoplistidae* sp7 showing no clear difference in total of calls observed between the two conditions (Online Resource 3).

The number of cricket species and calls observed in the recordings show lower values in invaded than in non-invaded area in all three habitat types (Fig. 4). The GLMM models explained 62.1 and 86% (R^2c values) of the variability of the number of species and the number of calls in nighttime recordings

respectively. These models showed a significant impact of the invasion by *W. auropunctata* on both the number of species and the number of calls observed in the nighttime recordings. The average number of species in sites without *W. auropunctata* was equal to the exponential intercept of the model 1 (4.32) and the average number of species in sites with *W. auropunctata* to the exponential of the intercept of the model added to the estimate of the factor level 'with *W. auropunctata*' (1.08) leading to a significant average difference of 3.24 species per recordings in presence of the invasive ant (likelihood ratio test: $\chi^2(1) = 16.39$, $p = 5.17e{-}05$). Similarly, the results of model 2 showed that the average number of calls in sites without *W. auropunctata* (110.79), and the average number of calls in sites with *W. auropunctata* (20.47) lead to a significant average difference of 90.32 calls per recordings between the two conditions (likelihood ratio test: $\chi^2(1) = 8.33$, $p = 0.004$).

Both NMDS ordinations in two dimensions—based on the presence/absence of the species and based on the calling song abundance of cricket species—showed that particular cricket species communities exist in the presence of *W. auropunctata* in forest and preforest with few or no overlaps. However, there is a large overlap of cricket communities from invaded and non-invaded shrublands (Fig. 5). Analysis of similarities (ANOSIM) supports this observation with significant dissimilarity in cricket community composition in forest using presence/absence of cricket species ($R^2 = 0.43$ $p = 0.031$) and abundance of calls per cricket species ($R^2 = 0.51$, $p = 0.034$), significant results in preforest using presence/absence of cricket species ($R^2 = 0.62$, $p = 0.037$) and abundance of calls per cricket species ($R^2 = 0.4$, $p = 0.033$), and non-significant results in shrubland using both presence/absence of cricket species ($R^2 = 0.51$, $p = 0.059$) and abundance of calls per cricket species ($R^2 = 0.3$, $p = 0.081$).

Results of the indicator species analysis identified the cricket species *A. azurensis* and *A. bouensis* ($p = 0.022$) as significant indicators of the ant invasion in forest, and *A. clarus*, *Mogoplistidae.* sp1 and *Mogoplistidae* sp2 ($p = 0.033$) in preforest. No species has been identified as indicator of the ant invasion in shrubland. Indicator species analyses conducted using the presence/absence data only identified *A. clarus* ($p = 0.032$) in preforest habitat, highlighting the importance of collecting the abundance of calls per species in this survey.
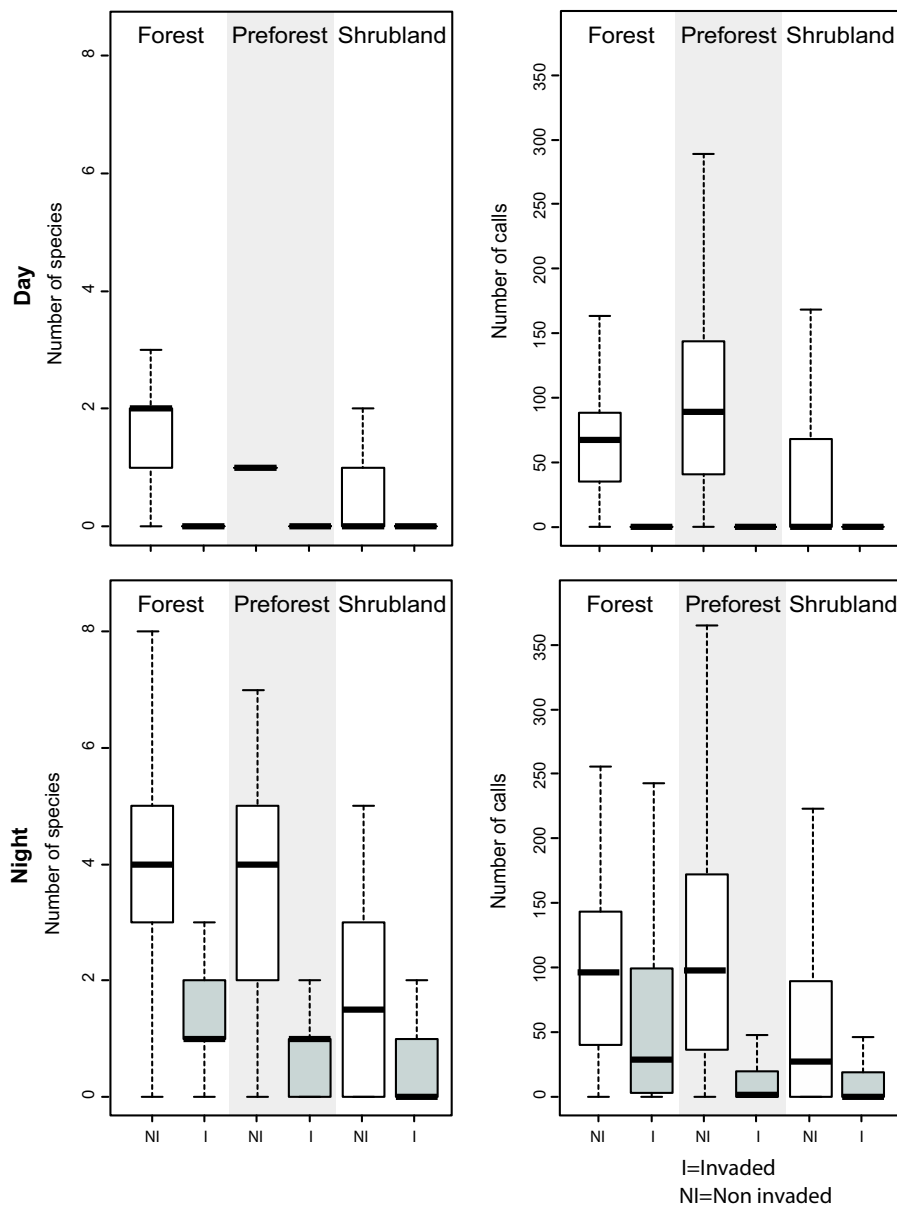
Fig. 4 Boxplots representing the number of cricket species and calls for each habitat and invaded modalities. The middle band inside the box represents the median value, the bottom and top of the box respectively the first (Q1) and third (Q3) quartiles and, the whiskers extend to points that lie within $Q1 - 1.5{*}IQR$ and $Q3 + 1.5{*}IQR$, IQR being the interquartile range between Q1 and Q3. Forest, preforest and shrubland free from invasive species are in blank plots, while invaded habitats by *Wasmannia auropunctata,* are in gray plots, for daytime and nighttime periods

Discussion

Ecoacoustic approaches that consist, among others, in recording and analyzing acoustic communities and soundscapes, offer applications for habitat surveys. Five arguments supporting the use of the cricket calling community as an indicator of the invasive ant, *W. auropunctata,* in New Caledonia are discussed.

First, research is establishing a solid referential knowledge of these cricket communities. From an effort devoted to the taxonomy and systematics of New Caledonia initiated 30 years ago, crickets have
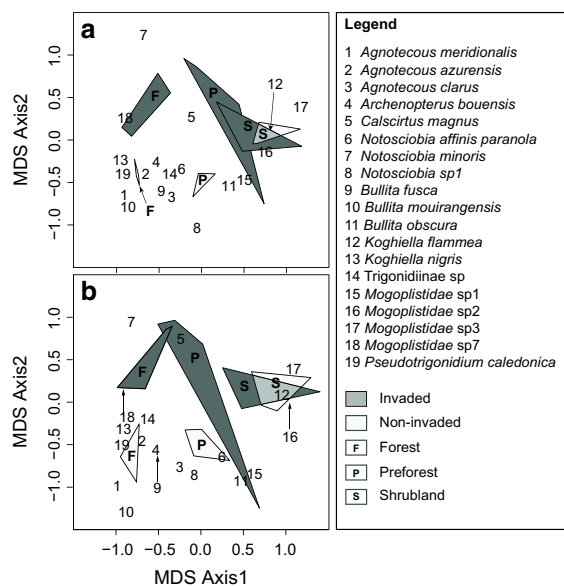
Fig. 5 NMDS (two dimensions) based on a-the presence and absence of cricket species acoustically identified (stress = 0.11) and b-the abundance of calls per cricket species (stress = 0.1). Polygons were drawn according to habitat type and ant invasion. Sites, such as FO-PDP, are labeled according to the habitat type (FO for forest, PA for preforest and MA for shrubland) and then according to the locality name (see Table S1 for additional information). The site MA-KA-W has been excluded from this analysis

been rapidly identified as one of the main putative model groups, with studies devoted to acoustic evolution (Robillard et al. 2007; Anso et al. 2016a), speciation (Nattier et al. 2012), and more recently, the succession of cricket communities in different habitats (Anso 2016). The results presented here are considered in the context of complementary taxonomic, ecological and acoustic knowledge acquisition of this group in New Caledonia (Anso 2016; Anso et al. 2016b; Desutter-Grandcolas et al. 2016).

Second, the abundance and dominance of detectable cricket calls in nighttime soundscapes has been demonstrated. Using soundscape descriptions, we could ascertain the presence of 19 of the 29 overall cricket species—both mute and acoustically active—described by complementary classic inventories made on the same site (Anso et al. 2016b). The cricket stridulations largely dominate the nighttime soundscapes, justifying the acoustic approach to detect environmental changes through the nocturnal acoustic activities of cricket communities. While cricket communities are known to be abundant in all tropical

systems (Riede 1993; Nischk and Riede 2001), their dominance in all tropical nighttime soundscapes still needs to be demonstrated in order to generalize this approach to other sites and other invasion contexts.

Third, the three habitat types were successfully discriminated by the acoustic signature of their cricket communities. From taxonomical inventories made on the same sites (Anso 2016; Anso et al. 2016b), we know that the entire cricket community (species producing or not producing calls) are habitat specific. Although the acoustic approach allows the detection of only a subset of the overall cricket community, the results of our acoustic study confirm that the acoustic-mediated species of the cricket community are sensitive to different environmental conditions (Desutter-Grandcolas 1992; Szinwelski et al. 2012), and that each habitat can be defined by a specific acoustic signature as shown in Bormpoudakis et al. (2013). More specifically, some cricket species have been recorded only in one habitat type, as documented for other Orthoptera in European/temperate countries (Schirmel et al. 2011; Fartmann et al. 2012). This suggests that the ecological distribution of cricket species may be restricted by particular microclimatic conditions (Gardiner and Dover 2008), environmental constraints for communication (Römer 1993), and/or micro-habitat availability (Jain and Balakrishnan 2011).

Fourth, results showed the significant effect of the presence of *W. auropunctata* on cricket acoustic activity in all habitats and on cricket community composition in forest and preforest habitat. These results could be supported by four different hypotheses: (1) a reduction in species number in the community, (2) a reduction in the number of individuals per species, (3) a targeted effect on some cricket species and/or (4) a change in the behavior of the species in the presence of the ant, leading to a decrease in acoustic activity. To the best of our knowledge, no survey has investigated the effects of invasive ants on any calling behavior. However, the spread of *W. auropunctata* generally negatively affects terrestrial invertebrates (Lubin 1984; Jourdan et al. 2001; Walker 2006). Complementary classic species inventory documented that the presence of the ant decreased both the number of individuals and the number of cricket species at the sites (Anso 2016). Two non-exclusive mechanisms could explain this decrease in species and individuals detected through acoustic activity. First, non-lethal

interactions by indirect competition for calling sites, shelter or food resources, or by territorial defensive attacks—*W. auropunctata* uses a poisonous stinger to repeal predators—could lead crickets to move and avoid the invaded area. A second mechanism could be lethal interactions by direct predation of the ant on eggs or small individuals, including juveniles. Interestingly, among the species not recorded in the invaded area, seven species were leaf litter-dwellers, suggesting a higher sensitivity to foraging ant workers than crickets perched on vegetation. In the same way, *Pseudotrigonidium caledonica*, a discrete forest species that perched on understory vegetation for calling, but may hide during the day in the leaf litter accumulated at the base of the plants, was not recorded in invaded areas. This pattern likely highlights the vulnerability of *P. caledonica* to *W. auropunctata*, perhaps during other activities, such as feeding, resting or copulating. According to our findings, four cricket species could be defined as acoustic flags revealing the presence of *W. auropunctata*: *A. azurensis* (daytime and nighttime) in forest; *A. clarus* (nighttime), *Mogoplistidae* sp1 and *Mogoplistidae* sp2 (nighttime) in preforest. However, we suspect other potential indicator species from our personal observations such as *B. mouirangensis* (daytime), *P. caledonica* (nighttime) and *A. meridionalis* (nighttime) in forests, *B. fusca* (daytime) and *B. obscura* (daytime) in forest and preforest habitats and, Mogoplistidae sp3 (nighttime) in shrubland, that could explain the difference in community composition observed between invaded and non-invaded sites.

Finally, this approach is non-invasive, easy to manage on large temporal and spatial scales and more affordable—in terms of cost and field work efforts—for conservation programs. As demonstrated here, only a few days of soundscape recordings were necessary to describe the cricket calling community. If taxonomic knowledge is necessary to manually identify the calls in the recordings, additional research could focus on the application of automatic recognition techniques. Automatic identification challenges are expected to be reduced because (1) nighttime New Caledonian soundscapes of the dry season do not present extensive signal overlaps and (2) cricket stridulations are easy to identify by classic acoustic features including duration, echeme number, frequency range, and dominant frequency, thanks to previous taxonomic inventory practices.

Future research is needed to confirm the use of acoustic approaches for the early detection of the alien species arrival, evaluation of the invasion level and monitoring of restoration processes. Increasing the number of sampled sites would allow building a predictive model and to determine the invasion of a site based on the composition of its cricket community. In the present study, we considered invaded versus non-invaded sites, but we suspect that some native species may have a different degree of resistance to invasion (Holway et al. 2002) that, once described, could allow scientists and managers to estimate the level of invasion from the cricket calling community composition at a given time. Finally, the influence of the invasive strategy—movement in independent patches or along a coherent front line—on the presence of "refugium" patches for cricket species needs to be investigated. To illustrate this issue, several species—genera *Koghiella* and *Agnotecous*—living in micro-habitats exposed to foraging ants (leaf litter, bare soil) were recorded in invaded areas. Nevertheless, the high reduction of the number of stridulations of these species between non-invaded and invaded areas show the relative role of these 'refugia'. Another bias that needs to be investigated is related to the long-range calls of canopy species in close-by modalities such as the easily identified canopy species *C. magnus* living in forest and preforest that was recorded in shrublands sites, due to the long-distance propagation of its call.

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Resource 1: Description of the vegetation criteria defining the three habitat types

The "forest" type is a dense forest with large stems, a deep leaf litter entirely covering the ground, a closed canopy and a maximum vegetation height at 30 m. The tree layer is composed of diverse dominant families, such as Araucariacea, Sapotacea, Myrtacae, and Proteacea. Palm trees, Pandanus and ferns dominate the shrub layer. The "preforest" type is similar to the "forest" type but with a lower vegetation height and plant species: the tree layer is characterized by an

assemblage of *Styphellia cymbulae*, *Hibbertia lucens*, *Alphitonia neaocaledonica*, and *Gymnostoma deplancheanum* and the herbaceous layer is dominated by *Lepidosperma perteres.* The "shrubland" type is characterized by high bare ground expanse and absence of a continuous tree layer. Maximum vegetation height was about 3 m with an important herbaceous and shrub layers dominated by *Sannantha* sp., *Eugenia* sp., *Alphitonia neocaledonica*, *Hibbertia lucens* and *H. pancheri*.

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Resource 2: Table S1. Site descriptions.

Site Code	Name	Habitat	Invaded (n/9)	Coordinates	Recording dates
FO-BOI-W	Port Boisé	Forest	Yes (7/9)	166.97343E/22.34820S	Oct. 23-Nov. 14
FO-FN-W	Foret Nord	Forest	Yes (9/9)	166.92987E/22.32372S	Oct. 03-Oct. 23
FO-GK-W	Grand Kaori	Forest	Yes (5/9)	166.89601E/22.28226S	Oct. 02-Oct. 30
FO-KA-W	Cap Ndua	Forest	Yes (9/9)	166.91742E/22.38645S	Oct. 17-Nov. 14
FO-GK	Grand Kaori	Forest	No (1/9)	166.89674E/22.28535S	Oct. 02-Oct. 10
FO-MOU	Mouirange	Forest	No (0/9)	166.68086E/22.20416S	Oct. 02-Oct. 17
FO-PDP	Pic du pin	Forest	No (0/9)	166.82715E/22.24680S	Oct. 03-Oct. 17
FO-RIV	Rivière Blanche	Forest	No (0/9)	166.68643E/22.15142S	Oct. 04-Oct. 17
MA-BDS-W	Bois du Sud	Shrubland	Yes (7/9)	166.76093E/22.17321S	Nov. 20-Dec 16
MA-GKE-W	Grand Kaori Ext.	Shrubland	Yes (9/9)	166.86960E/22.27110S	Oct. 23-Nov. 14
MA-KA-W	Cap Ndua	Shrubland	Yes (8/9)	166.93486E/22.32278S	Oct. 17-Nov. 14
MA-RIV-W	Rivière Blanche	Shrubland	Yes (6/9)	166.70937E/22.13480S	Oct. 17-Nov. 07
MA-MAD	Madelaine	Shrubland	No (0/9)	166.85268E/22.23568S	Oct. 17-Nov. 14
MA-FN	Forest Nord	Shrubland	No (2/9)	166.93501E/22.32277S	Oct. 23-Nov. 14
MA-GK	Grand Kaori	Shrubland	No (2/9)	166.89436E/22.28460S	Oct. 02-Oct. 17
MA-RIV	Rivière Blanche	Shrubland	No (3/9)	166.70796E/22.13625S	Oct. 04-Oct. 17
PA-FN-W	Foret Nord	Preforest	Yes (9/9)	166.93361E/22.32385S	Oct. 03-Oct. 23
PA-GK-W	Grand Kaori	Preforest	Yes (7/9)	166.89510E/22.28345S	Oct. 02-Oct. 30
PA-KA-W	Cap Ndua	Preforest	Yes (9/9)	166.91881E/22.38629S	Oct. 17-Nov. 14
PA-PRO-W	Prony	Preforest	Yes (8/9)	166.80473E/22.31902S	Oct. 23-Nov. 15
PA-FN	Forêt Nord	Preforest	No (4/9)	166.93134E/22.32259S	Oct.03-Oct. 23
PA-GK	Grand Kaori	Preforest	No (0/9)	166.89383E/22.28000S	Oct.02-Oct. 20
PA-PEP	Pépinière	Preforest	No (0/9)	166.96355E/22.27103S	Oct. 02-Oct. 17
PA-RIV	Rivière Blanche	Preforest	No (0/9)	166.68033E/22.15280S	Oct. 04-Oct. 17

Sites are considered as Invaded if n<5 with n the number of observation of *W. auropunctata* around the recorder.

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Resource 3:

Table S2. Summary of acoustic observations from soundscape recordings for each cricket species and on non-invaded and invaded sites separately.

Species	Non-invaded sites			Invaded sites		
	Rec. num.	Call num.	Av. call per rec. (sd.)	Rec. num.	Call num.	Av. call per rec. (sd.)
Agnotecous azurensis	381	2851	7.48 (5.43)	64	309	4.83 (3.12)
Agnotecous clarus	88	630	7.16 (4.04)	0	0	0
Agnotecous meridionalis	21	91	4.33 (2.85)	0	0	0
Archenopterus bouensis	342	5648	16.51 (12.26)	9	42	4.67 (6.26)
Bullita fusca	330	28952	87.73 (62.50)	0	0	0
Bullita mouirangensis	60	5106	85.1 (26.42)	0	0	0
Bullita obscura	67	5634	84.09 (49.83)	0	0	0
Calcirtus magnus	421	13832	32.86 (35.27)	360	10787	29.96 (31.97)
Koghiella flammea	312	19702	63.15 (45.29)	32	1115	34.84 (26.25)
Koghiella nigris	211	2463	11.67 (9.65)	19	390	20.53 (25.67)
Trigonidiinae sp	40	6272	156.8 (53)	47	4002	85.15 (36.88)
Mogoplistidae sp1	205	11115	54.22 (51.39)	67	3758	56.09 (38.20)
Mogoplistidae sp2	221	4970	22.49 (20.04)	77	1123	14.58 (12.68)
Mogoplistidae sp3	85	3346	39.36 (33.12)	0	0	0
Mogoplistidae sp7	74	2775	37.5 (39.10)	56	2807	50.125 (33.63)
Notosciobia affinis paranola	100	8153	81.53 (57.61)	51	1163	22.80 (23.02)
Notosciobia minoris	1	45	45	61	6870	112.62 (57.94)
Notosciobia sp1	3	1006	335.33 (56.13)	0	0	0
Pseudotrigonidium caledonica	71	580	8.17 (4.21)	0	0	0

"Rec". calls for "recording", "num." for "number", "av." for "average", and "sd." for "standard deviation"
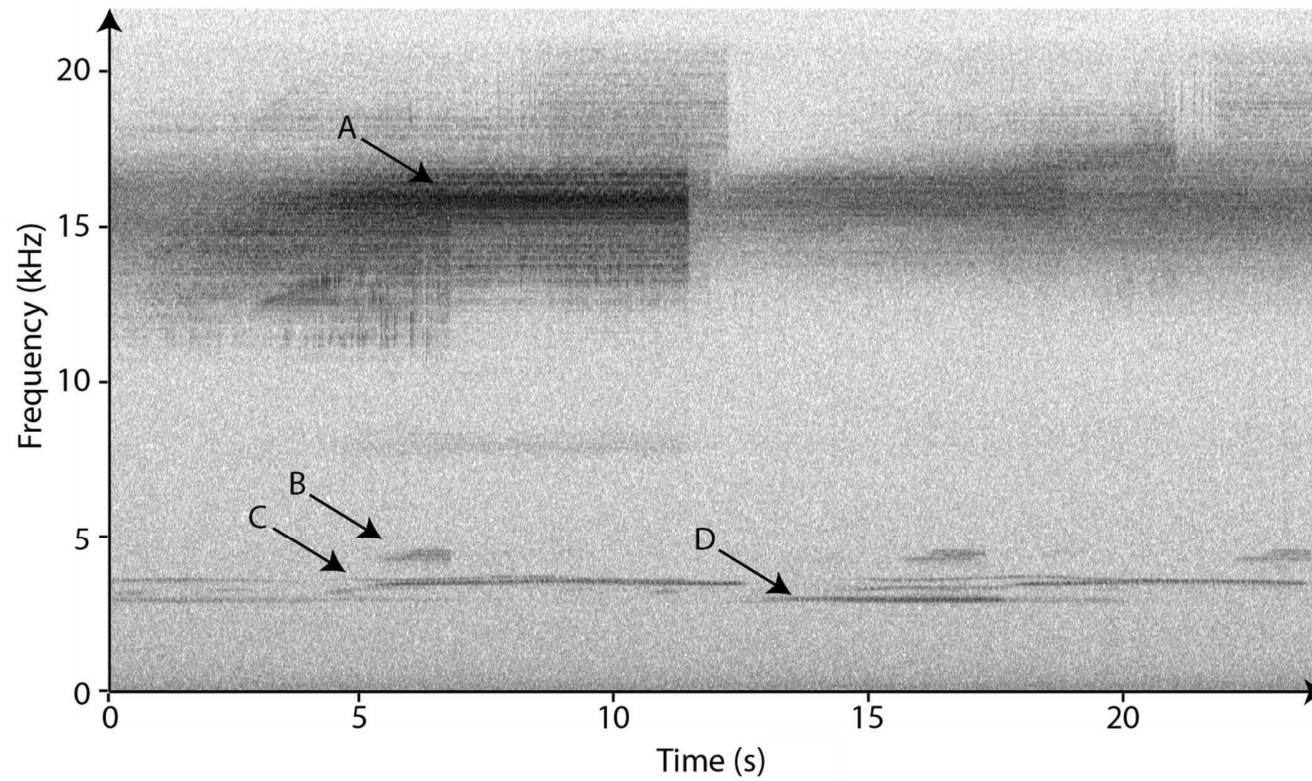
Fig. S1. Spectrogram of one recording from the non-invaded forest site "Pic du Pin" by night at 9 p.m. Four species were calling here: A calls for *Agnotecous azurensis* (six calls), B for *Koghiella nigris* (three calls), C for *Archenopterus bouensis* (four calls), and D for *Pseudotrigonidium caledonica* (two calls).

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Resource 4: Information concerning the models.

Model information

The description of the models follows the recommendations given by Nakagawa et al. (2013). This description is complemented here by the validation steps presented in the materials and methods.

1) Mathematical description of the models

Formulae for the model 1:

Distribution-specific variance: $\ln(1/\exp(\beta_0)+1)$

$$y_{ijkl} = Poisson(\mu_{ijkl})$$

$$link(\mu_{ijkl}) = \beta_0 + \sum_{h=1}^{2} \beta_h S_{hijkl} + \alpha_j + \delta_k + \gamma_l + \varepsilon_{ijkl} \qquad (1)$$

where y_{ijkl} is the *i*th *count of species* at the *j*th *site* at the *k*th *date* and the *l*th *time* , μ_{ijkl} is the underlying (latent) mean for the *i*th *count of species* at the *j*th *site* at the *k*th *date* and the *l*th *time*, β_0 is the intercept, β_h is the slope of the *h*th predictor (*h*=1 represent the invasion factor and *h*=2 represent the habitat factor), X_{hijkl} is the *i*th values *j*th site at the *k*th *date* and the *l*th *time* for the *h*th predictor, α_j is the *site* specific effect following a normal distribution of mean 0 and variance σ_α, δ_k id the *date* specific effect following a normal distribution of mean 0 and variance σ_δ, γ_l is the *time* specific effect following a normal distribution of mean 0 and variance σ_γ and ε_{ijkl} is the residual following a normal distribution of mean 0 and variance σ_ε. This model has been implemented in R as follows: *glmer(SpeciesNumber ~ invasion + habitat + (1|site) + (1|date) + (1|time), family=poisson)*

Formulae for the R² for Poisson model 1:

Given σ_{f1}^2, the variance of the fixed effect components of the model 1, we calculated the

marginal R^2 (R^2_{m1}) and the conditional R^2 (R^2_{c1}) of the model 1 as follows:

$$\sigma_{f1}^2 = \mathrm{var}(\sum_{h=1}^{2} \beta_h S_{hijkl})$$

$$R^2_{m1} = \frac{\sigma_{f1}^2}{\sigma_f^2 + \sigma_\alpha^2 + \sigma_\delta^2 + \sigma_\gamma^2 + \sigma_\varepsilon^2 + \ln(1/\exp(\beta_0 + 1))}$$

$$R^2_{c1} = \frac{\sigma_{f1}^2 + \sigma_\alpha^2 + \sigma_\delta^2 + \sigma_\gamma^2}{\sigma_{f1}^2 + \sigma_\alpha^2 + \sigma_\delta^2 + \sigma_\gamma^2 + \sigma_\varepsilon^2 + \ln(1/\exp(\beta_0 + 1))}$$

Formulae for the model 2:

Link function: log link

Distribution-specific variance: $\ln(1/\exp(\lambda_0) + 1)$

$$z_{ijk} = Poisson(\kappa_{ijk})$$

$$link(\kappa_{ijk}) = \lambda_0 + \sum_{h=1}^{2} \lambda_h C_{hijk} + a_j + b_k + c_{ijk} \tag{2}$$

where z_{ijkl} is the *i*th *count of calls* at the *j*th *site* at the *k*th *date*, κ_{ijkl} is the underlying (latent)

mean for the *i*th *count of calls* at the *j*th *site* at the *k*th *date*, λ_0 is the intercept, λ_h is the slope of

the *h*th predictor (*h*=1 represent the invasion factor and *h*=2 represent the habitat factor), C_{hijk} is

the *i*th value *at the j*th *site* at the *k*th *date* for the *h*th predictor, a_j is the *site* specific effect

following a normal distribution of mean 0 and variance σ_a, b_k id the *date* specific effect

following a normal distribution of mean 0 and variance σ_b and c_{ijk} is the residual following a

normal distribution of mean 0 and variance σ_c. This model has been implemented in R as

follows: *glmer(CallNumber ~ invasion + habitat + (1|site) + (1|date), family=poisson)*

Formulae for the R^2 for Poisson model 2:

Given σ^2_{f2} the variance of the fixed effect components of the model 2, we calculated the marginal R^2 ($R^2{}_{m2}$) and the conditional R^2 ($R^2{}_{c2}$) of the model 2 as follows:

$$\sigma^2_{f2} = \mathrm{var}(\sum_{h=1}^{2} \lambda_h C_{hijk})$$

$$R^2{}_{m2} = \frac{\sigma^2_{f2}}{\sigma^2_{f2} + \sigma^2_a + \sigma^2_b + \sigma^2_c + \ln(1/\exp(\lambda_0 + 1))}$$

$$R^2{}_{c2} = \frac{\sigma^2_{f2} + \sigma^2_a + \sigma^2_b}{\sigma^2_{f2} + \sigma^2_a + \sigma^2_b + \sigma^2_c + \ln(1/\exp(\lambda_0 + 1))}$$

2) Results and validations of the models

The results of the models are available in the Table S3. For each model, we tested for deviation of the residuals from 1) linearity, homoscedasticity and normality by visual inspection of the relationship of residuals against fitted values and the quantile-quantile plot of residuals, and 2) the absence of collinearity between the fixed effects by looking at the Generalized Variation Inflation Factor (Fox and Monette, 1992) calculated with the function vif from the R car package (Fox and Weisberg, 2011). Time seemed to have a negative effect on the linearity of the residuals of the model 2 that has been corrected by removing this factor of the model. The Generalized Variation Inflation Factor looking at the absence of the collinearity between the fixed effects is presented in the Table S4. Validation of linearity, homoscedasticity and normality of the residuals can be visual inspected by looking at the plots of the residuals against fitted values and the Quantile-Quantile plot of residuals presented in the Figure S2.

Table S3: Results of the Generalized mixed models.

	Model1	Model2
Fixed effects	Estimates (SD)	Estimates (SD)
Intercept	1.4633 (0.3044)	4.7076 (0.5684)
Invasion (With)	-1.3822 (0.2827)	-1.6887 (0.5398)
Habitat (Shurbland)	-1.1154 (0.3474)	-1.5645 (0.6543)
Habitat (Paraforest)	-0.4847 (0.3416)	-0.5598 (0.6345)
Random effects	Variance (SD)	Variance (SD)
Site	0.454168 0.6739	-
Date	0.001 (0.0286)	0.586 (0.7653)
Time	0.1506 (0.388)	1.628 (1.2760)
R^2m	0.3873315	0.5370056
R^2c	0.6208671	0.8607849
AIC	3817.386	57810.73
BIC	3838.475	57826.54

"SD" calls for standard deviation

Table S4: Generalized Variation Inflation Factor (GVIF) results, similar for both models.

	GVIF	Df	$GVIF^{(1/(2*Df))}$
Envahis	1	1	1
Habitat	1	2	1

Literature Cited

Fox J, Monette G. 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association **87**:178–183.

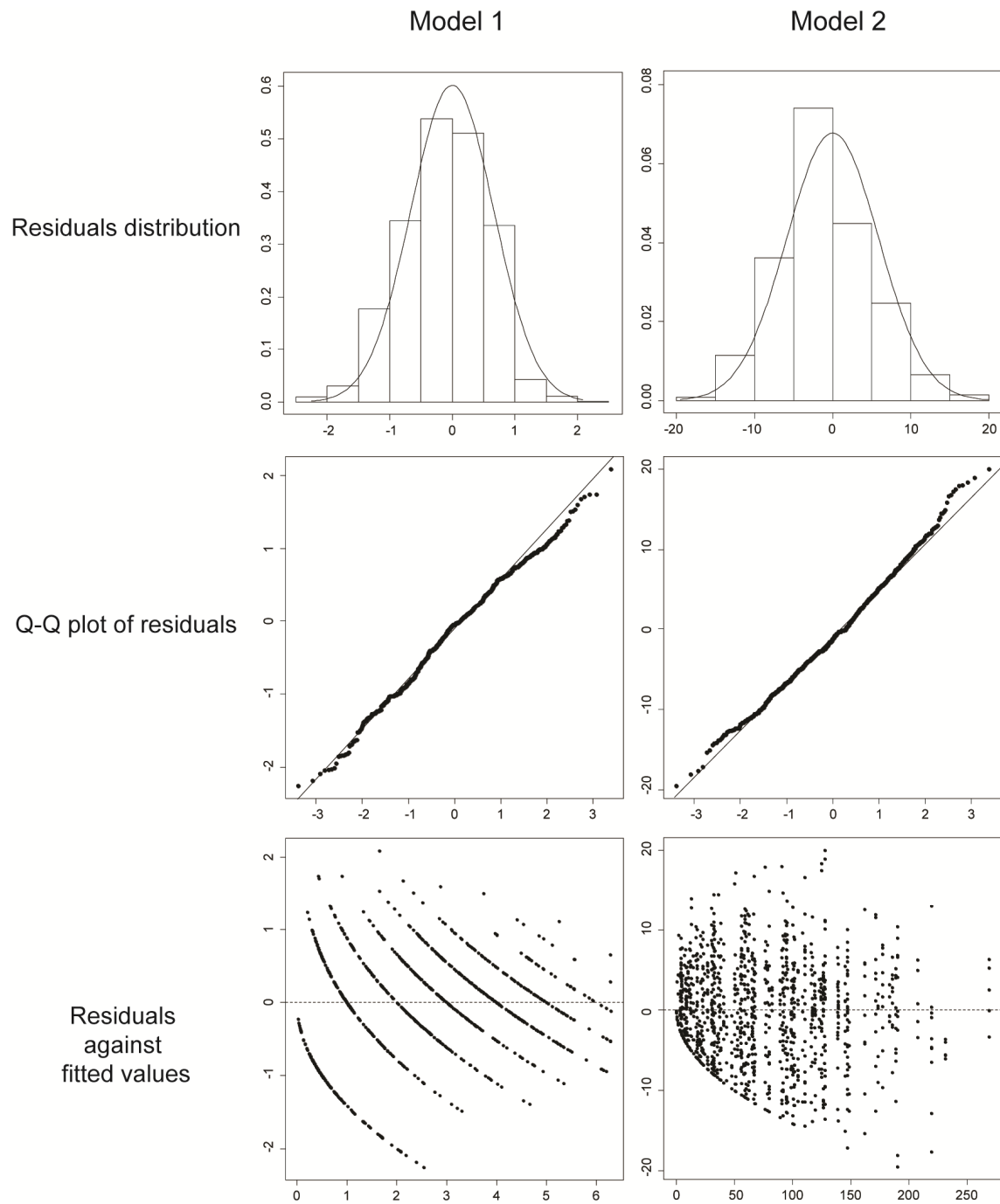Fox J, Weisberg S. 2011. An R Companion to Applied Regression, second ed. Sage, Thousand Oaks CA.

Figure S2. Three graphics for the inspection of the residuals of the models 1 and 2: the histogram of the residuals, the Quantile-Quantile plot of residuals and the plot of the residuals against the fitted values.