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ORIGINAL ARTICLE

Crickets as indicators of ecological succession in tropical systems, New Caledonia

Jeremy Anso[1,2] | **Amandine Gasc**[1] | **Edouard Bourguet**[1] | **Laure Desutter-Grandcolas**[2] | **Hervé Jourdan**[1]

[1]CNRS, IRD, IMBE, BPA5, Aix Marseille Univ, Avignon Univ, Nouméa Cedex, New Caledonia

[2]CNRS, UMPC, EPHE, UA, Institut de Systématique, Evolution, Muséum National d'Histoire Naturelle, Sorbonne Universités, Paris Cedex 05, France

Correspondence
Amandine Gasc, CNRS, IRD, IMBE, BPA5, Aix Marseille Univ, Avignon Univ, 98848 Nouméa Cedex, New Caledonia.
Email: amandine.gasc@ird.fr

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Abstract

Crickets (Ensifera, Grylloidea) are not commonly used as ecological indicators in contrary to other Orthoptera (e.g., grasshoppers and katydids). However, they are sensitive to environmental changes and abundant in tropical regions. To evaluate whether crickets are relevant bioindicators of tropical ecosystems, we investigated cricket assemblages along a tropical ecological gradient. We collected crickets during both day and night in southern New Caledonia for three stages of ecological succession: open shrubland, preforest, and forest. Simultaneously, we measured several environmental variables, such as temperature and relative humidity, at each sampling site. Cricket species assemblages showed a clear response to ecological succession. The highest and lowest species richness and abundances of individuals were, respectively, found in forest and shrubland, with species specialized in each ecological stage revealing the conservation value of each of these stages. Similar results were found when considering only the part of cricket communities with the ability to acoustically communicate. This work is part of a larger research program about Neocaledonian crickets and contributes to support the use of acoustic approaches to monitor tropical environments. In conclusion, these findings highlight the potential value of crickets as an environmental indicator in tropical ecosystems. The results also contribute to the discussion of the intrinsic conservational value of shrublands in New Caledonia and similar ecotypes.

Abstract in French is available with online material.

KEYWORDS
bioindicator, community ecology, conservation, crickets, ecoacoustics, ecological succession, taxonomic inventory, tropics

1 | INTRODUCTION

Global biodiversity is experiencing a major crisis (Barnosky et al. Barnosky et al., 2011; Ceballos et al., 2015), where habitat fragmentation and loss are drivers in the reduction of population and extinction of species (Brook et al., 2008; Brooks et al., 2002; Hoekstra et al., 2005). Regions with significant levels of biodiversity, which are increasingly threatened, deserve special attention

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for conservation and restoration (Dawson et al., 2014; Mittermeier et al., 2011; Myers et al., 2000). Conservation programs often rely on biodiversity monitoring using diversity indices (Barlow et al., 2007). Two of the most common diversity indices are species richness and evenness (Ricotta, 2005). Such diversity indices are dependent upon species inventories, which are time-consuming (Lawton et al., 1998), expensive, and require highly skilled specialists (Levrel et al., 2010). The United Nations has therefore strongly encouraged the scientific community to develop biodiversity indicators for biodiversity conservation (Strategic Plan for Biodiversity 2011–2020, United Nations, 2020, IPBES, 2019).

Bioindicators are generally used to assess environmental change, to monitor specific disturbances, or to estimate taxonomic diversity (Gerlach et al., 2013; McGeoch et al., 2011). Such indicators serve several applications, including assessing the condition of the environment (Niemi & McDonald, 2004), following ecosystem restoration programs (Alignan et al., 2014), or prioritizing the management of habitats (Fartmann et al., 2012). The challenge in selecting taxa as bioindicators in complex habitats, such as tropical forests, is that they require sufficient knowledge about their distributions and natural fluctuations, with a fairly resolved taxonomic knowledge. This is frequently absent in tropical environments (Moritz et al., 2001).

Among invertebrates, Orthoptera (spanning greater than 28,000 valid species; Cigliano et al., 2020) are widely used to assess ecological or environmental changes (Gerlach et al., 2013). They are a key resource for upper food web species, such as lizards, spiders, and birds (Borges et al., 2013; Pretelli et al., 2014; Shea et al., 2009; Taylor et al., 2012) and play an important role in recycling organic matter (Prather et al., 2013). Related to ecological changes, Orthoptera species richness and composition have been negatively associated with mowing and grazing (Rada et al., 2014; Rambo & Faeth, 1999), and they are regularly used to assess the success of restoration programs (Alignan et al., 2014, 2018; Hugel, 2012; Rácz et al., 2013). Among Orthoptera, grasshoppers and katydids are commonly used to assess environmental change and restoration in temperate regions where they are well-diversified and can be easily identified, especially in open habitats (Fartmann et al., 2012; Marini et al., 2009; Schirmel et al., 2011). Grasshoppers were also found to be markers for forest succession in Western Amazonia (Amédégnato, 1997; Amédégnato & Descamps, 1980).

Crickets (Orthoptera, Grylloidea) are the other large group of Orthoptera, with approximately 6000 species (Cigliano et al., 2020). Crickets are studied as models in ethology, neurobiology, physiology, and bioacoustics (Gerhardt & Huber, 2002; Kulkarni & Extavour, 2019) but receive less focus in ecology. Most ecological studies assessing restoration or habitat management using Orthoptera assemblages have not separated grasshoppers, katydids, and crickets. In particular, only a few have considered the cricket community alone (e.g., Hoffmann et al., 2002; Szinwelski et al., 2012). While underexplored, crickets as potential bioindicators in the endangered tropics hold significant potential because of their high level of diversification and endemism in the tropics (Cigliano et al., 2020), abundance, and local ecological specializations (Desutter-Grandcolas, 1995, 1997), and use of recognizable acoustic signals (Anso, Jourdan, & Desutter-Grandcolas, 2016; Diwakar & Balakrishnan, 2007) when using passive acoustics for monitoring.

The goal of the present study was to evaluate whether crickets, at the species and community level, might be qualified as relevant bioindicators of tropical ecosystems. The effect of vegetation and bioclimatic attributes along shrubland to forest gradient on cricket assemblages was assessed. Research was performed in New Caledonia, which was advantageous for two reasons. First, a detailed description of the cricket species living in the area of interest was needed (Anso, Jourdan, & Desutter-Grandcolas, 2016; Desutter-Grandcolas et al., 2016), and second, New Caledonia is representative of various tropical ecosystems. Crickets represent a well-diversified part of the original and disharmonic insect fauna of New Caledonia (Grandcolas et al., 2008), with 40 genera and more than 180 species recorded today in the archipelago. A total of 19 of the genera and more than 90% of the species are endemic to the territory (Desutter-Grandcolas et al., 2016). Guessestimate of the total richness of the cricket fauna, based on the putative pattern of species assemblage in New Caledonia (Anso, Jourdan, & Desutter-Grandcolas, 2016), leads to the hypothesis that the actual number of crickets in New Caledonia should be much more important, especially because of the high microendemism that characterizes this fauna (Grandcolas et al., 2008; Nattier et al., 2011). Nevertheless, the cricket fauna living in our research area is well described (Anso, Jourdan, & Desutter-Grandcolas, 2016; Desutter-Grandcolas et al., Desutter-grandcolas et al., 2016). New Caledonia is additionally a biodiversity hotspot (Myers et al., 2000), with a high endemism rate (Grandcolas et al., 2008), and experiences multiple disturbances, including species invasion, and habitat loss (Ibanez et al., 2019; Jaffré, Bouchet, & Veillon, 1998; Jaffré, Rigault, & Dagostini, 1998; Pellens & Grandcolas, 2009). Therefore, furthering ecological knowledge in this context holds high value for local conservation plans by helping to evaluate forest restoration programs, which are of high importance due to mining activity in New Caledonia (Losfeld et al., 2014).

In this study, a large taxonomic inventory was conducted during both day and night to measure the overall abundance, species richness, composition, and structure of the cricket communities. Data were collected in three ecological stages defined by a gradient of microclimate and vegetation characteristics (forest, preforest, and shrubland) in the south of the New Caledonian archipelago's main island, on ultramafic soil. New Caledonian ecosystems are not naturally fire-prone ecosystems (McCoy et al., 1999; Stevenson et al., 2001), but fire is promoted by human populations since their arrival. Ultramafic substrates are characterized by low nutriment and slow vegetation growth (Isnard et al., 2016; Pillon et al., 2021), several decades according to McCoy et al. (1999) and Pillon et al. (2021). On these soil compartments, the succession is marked by the transition from open shrubland to arbustive shrubland to preforest to forest stages. Each stage shows clear-cut vegetation formation in terms of stem density, litter cover, and stratification (Jaffré, Rigault, & Dagostini, 1998; McCoy et al., 1999). The context of succession on ultramafic soils is similar to South Africa and Southwest Australia, with shrubland that resembles the South African fynbos or the Southwest Australian kwongankaroo (Pillon et al., 2021).

Analyzing these data, the following questions were addressed: (1) Are assemblages of crickets following the ecological succession? (2) Are any specific cricket species an indicator of the ecological stages? And (3) is acoustic monitoring a suitable method for the evaluation of the ecological stages? This research is part of a larger research program conducted in New Caledonia focusing on biodiversity monitoring using taxonomic and acoustic methods. The results will thus be interpreted and discussed within the larger findings of this program. In particular, a section of the discussion will be dedicated to Passive Acoustic Monitoring (PAM) (Sugai et al., 2019) for extracting information about the cricket community indicating their tropical habitat.

2 | METHODS

2.1 | Study sites

Cricket communities were studied in the southern region of Grande Terre, the main island of New Caledonia, an archipelago located in the Southwest Pacific Ocean. Sites were selected along the same geological ultramafic substrate at low altitude (231 ± 66 m; Table 1). To study the ecological succession of cricket fauna, three vegetation stages—forest, preforest, and shrubland—were considered. Four sites were chosen within each stage for a total of twelve sites.

Forests on the island consist of trees with large stems, a deep leaf litter entirely covering the ground, a closed canopy, and a maximum vegetation height of 30 m. The tree layer is composed of diverse, dominant families, such as Araucariaceae (*Agathis* sp. and *Araucaria* sp.), Sapotaceae (*Iteiluma* sp., *Planchonella* sp., and *Pichonia* sp.), Myrtaceae (*Syzigium* sp. and *Eugeania* sp.), and Proteaceae (*Kermadecia* sp. and *Macadamia* sp.). Several unidentified species of palm trees, pandanus, and ferns dominate the shrub and herbaceous layers of the forest.

TABLE 1 Location and GPS information of the 12 sites. The coordinate reference system used was WGS84

Location	Habitat	Longitude East	Latitude South
Forêt Nord	Shrubland	166.93501	22.32277
Grand Kaori	Shrubland	166.89436	22.28460
Chute de la Madelaine	Shrubland	166.85268	22.23568
Rivière Blanche	Shrubland	166.70796	22.13625
Forêt Nord	Preforest	166.93134	22.32259
Grand Kaori	Preforest	166.89383	22.28000
Pépinière	Preforest	166.96355	22.27103
Rivière Blanche	Preforest	166.68033	22.15280
Grand Kaori	Forest	166.89674	22.28535
Mouirange	Forest	166.68086	22.20416
Pic du Pin	Forest	166.82715	22.24680
Rivière Blanche	Forest	166.68643	22.15142

Preforest can be as dense as the forest but is composed of different plant species, characterized by a greater canopy openness and lower diameter tree stems. As in the forest, the bare ground is covered. The tree layer of preforest includes an assemblage of *Styphelia cymbulae*, *Hibbertia lucens*, *Alphitonia neaocaledonica*, and *Gymnostoma deplancheanum*, while the herbaceous layer is dominated by *Lepidosperma perteres*.

Shrubland is characterized by a high bare ground expanse and an absence of a continuous tree layer. More specifically, shrublands encompass small patches of vegetation with a thin leaf litter, separated by bare ground. The maximum vegetation height is around 3 m. Shrublands were dominated by shrubs but also include herbaceous species such as *Sannantha sp.*, *Eugenia sp.*, *Alphitonia neocaledonica*, *Hibbertia lucens*, and *H. pancheri*.

2.2 | Cricket sampling

Crickets were collected between November 2013 and April 2014. In each of the twelve sites selected (see section 2.1), two squared parcels with 10 m sides were delimited. Sampling was performed under clear sky meteorological conditions from hours 0900 to 1700 by day, and 1900 to 0000 by night. On each parcel, crickets were collected using the same collection method of ten 30-minute sessions, with five total collections by day and five by night. Crickets were located using both sight and song cues in the field only based on human perceptions, which is the most appropriate sampling method for crickets (Touroult et al., 2021). Another common method to collect insects seems inefficient for crickets (Touroult et al., 2021) such as (1) light trap that rarely attracts crickets, (2) pitfall that only captures specimens foraging in the leaf litter, (3) fogging, a method previously tried in New Caledonia leading to collecting mostly juveniles that could not be identified (LDG, pers. obs), or (4) interception trap that captures only flying insects, very rarely crickets. For each individual, activity (e.g., singing, eating, mating, resting) and microhabitat (e.g., trunk, leaf litter, vegetation, rocks, height from ground) were noted before the capture. Collected specimens were kept for identification, as most revealed new species to science (Anso, Jourdan, & Desutter-Grandcolas, 2016). Specimens are deposited in the Museum national d'Histoire naturelle de Paris with a reference collection in the Nouméa IRD center in New Caledonia. Species identifications were performed in the laboratory by comparison with the specimens in the deposited collections and using the classification derived from the extensive molecular phylogeny of crickets (Chintauan-Marquier et al., 2015). Based on previous taxonomic descriptions including acoustic production (i.e., Anso, Jourdan, & Desutter-Grandcolas, 2016; Desutter-grandcolas et al., 2016), we were able to attribute to each species a presence or absence of singing abilities. Of the 1030 individuals collected, 54 were discarded from the analyses. These specimens were not identifiable at the species level because of their destruction due to unfavorable conservation conditions (56%) or from the absence of morphological information for crickets in the juvenile development stage (44%). A table of the cricket inventory (Table S1) and the list of species full names (Table S3) are provided in the supplementary information.

2.3 | Environmental variables

During cricket sampling, environmental attributes were measured in each parcel, including the percentage of bare ground, the percentage of three vegetation layers (herbaceous, shrub, and tree), the number and diameter (dbh) of stems, the vegetation height, and the plant species richness. Canopy openness was extracted from photos taken with a 180° hemispherical (fisheye) lens in each parcel corner and in its center. From the photos, canopy openness was then calculated using the Gap Light Analyzer software (version 2.0, Simon Fraser University, Cary Institute of Ecosystem Studies) by estimating the percentage of light in the forest overstorey (Frazer et al., 1999). Daily temperature (°C) and relative humidity (%) were recorded every 30 minutes for 15 days at a 50-cm height above the ground using waterproof thermo-hygrometer sensors (HOBO U23 Pro v2; HOBOware software). A table of the environmental variables is available in the Supplementary Information (Table S2).

2.4 | Statistical analysis

Two datasets were created for statistical analyses. The first included the environmental attributes averaged per site, while the second described the cricket assemblages, defined here as the number of individuals per species averaged per site. All statistical analyses were performed using R (software; R Core Team, 2019), with the type I error set at 5%.

To evaluate differences between ecological stages a Kruskal–Wallis test followed by the post hoc Conover test for multiple comparisons with the Bonferroni correction was applied (Conover & Iman, 1979). This test was run separately on species richness (number of species), overall abundance (total number of individual crickets), and environmental variables. This test was computed using the function *posthoc.kruskal.conover.test* of the "PMCMR" R package (Pohlert, 2014).

To visualize the differences in cricket assemblages along the ecological succession, a Nonmetric Multidimensional Scaling (NMDS) was performed on cricket assemblages across sampling sites (Legendre & Legendre, 2012; Minchin, 1987). The Bray–Curtis distances of cricket assemblage were calculated between sites. NMDS analysis with 1000 iterations and two dimensions was then performed on each of these distance matrices. To explain each of the four NMDS observations, the environmental variables were fitted into ordination, and their significance was assessed with a permutation test ($n = 999$ permutations). The percentage of variance in cricket assemblages that can be explained by the ecological stages was assessed with a permutation test ($n = 999$ permutations) applied to the same Bray–Curtis distance matrix. This analysis was similarly conducted on cricket assemblages and summarized in four ways: (1) cricket species abundances, (2) stridulatory cricket species abundances, (3) presence or absence of cricket species, and (4) presence or absence of stridulatory cricket species. The function *metaMDS* was used to perform the Bray–Curtis distance and the NMDS analyses, while the permutation test was performed using the function *envfit* for environmental data. Lastly, the permutation test applied on the distance matrix of cricket assemblages was performed using the function *adonis*. These three functions are from the "vegan" R package (Oksanen et al., 2019). The function *s.class* from the "ade4" R package was used for the graphical scatter diagram representation of the ecological stages in the NMDS space (Dray & Dufour, 2007).

The beta diversity (β) of cricket assemblages measured as the Sorensen dissimilarity was partitioned in the turnover (β_{SIM}) and the nestedness (β_{NES}) components, being, respectively, the Simpson dissimilarity and the nestedness-resultant fraction of Sorensen dissimilarity. Abundances were first reduced to a simple presence or absence of the cricket species at each site. Then, their overall beta diversity was partitioned using the function *beta.multi* from the "betapart" R package (Baselga et al., 2012; Baselga & Orme, 2012). The same analysis was conducted on the presence or absence of the cricket species for each ecological stage.

To evaluate the most relevant species between paired ecological stages, a similarity percentage analysis (SIMPER) was performed on both the abundances per cricket species and the presence or absence of cricket species (Clarke, 1993; Warton et al., 2012). The Bray–Curtis dissimilarity was decomposed in species contribution. This analysis was performed using the function *simper* to the "vegan" R package (Oksanen et al., 2019). The R code used to compile, manipulate, and analyze the data is available as Appendix S4 and https://github.com/agasc/Anso-et-al-2022-Biotropica.

3 | RESULTS

3.1 | Cricket species along the succession

A total of 976 specimens, 30 species, and 16 genera were collected, belonging to four families (Gryllidae, Phalangopsidae, Trigonidiidae, and Mogoplistidae) and six subfamilies (Table 2). The most abundant species were *Bullita fusca* (Gorochov, 1986) and *Agnotecous azurensis* Desutter-Grandcolas, 2006 in both forest (40% and 31%, respectively) and preforest stages (35% and 25%, respectively). In shrublands, *Koghiella flammea* Anso & Desutter-Grandcolas, 2016 was the most abundant species (88%). Species richness increased gradually along the ecological succession, from the lowest number of species in shrubland (7 species), followed by observed increases in preforest (15 species) and forest (20 species) (Figure 1). Each ecological stage was additionally found to harbor exclusive species. Forest demonstrated the highest ratio of unique species (60% including 12 species) followed by shrublands (43% including 3 species) and preforest (14% including 2 species). Forest and preforest shared eight species,

TABLE 2 List of cricket species from the taxonomic inventory in alphabetical order. The symbol [a] indicates the number of specimens collected

Family	Subfamily	Species	Habitat ([a])	Microhabitat	Stridulatory	Capture time ([a])
Gryllidae	Eneopterinae	*Agnotecous azurensis*	Fo (143) / Pr (137)	Leaf litter	yes	Day (102) / Night (178)
Gryllidae	Eneopterinae	*Agnotecous clarus*	Fo (1) / Pr (34)	Leaf litter	yes	Day (7) / Night (28)
Gryllidae	Eneopterinae	*Agnotecous meridionalis*[b]	Fo (16)	Leaf litter	yes	Day (9) / Night (7)
Gryllidae	Eneopterinae	*Pixibinthus sonicus*	Pr (16) / Sh (5)	Leaf litter	yes	Day (11) / Night (10)
Gryllidae	Gryllinae	*Notosciobia affinis paranola* [c]	Pr (1)	Leaf litter/ burrows	yes	Night (1)
Gryllidae	Gryllinae	*Notosciobia minoris*	Fo (1) / Pr (1)	Leaf litter/ burrows	yes	Day (1) / Night (2)
Gryllidae	Gryllinae	*Notosciobia sp1*[b]	Fo (2)	Leaf litter/ burrows	yes	Day (2)
Gryllidae	Podoscirtinae	*Adenopterus crouensis*[d]	Sh (1)	Understory	no	Night (1)
Gryllidae	Podoscirtinae	*Adenopterus meridionalis*[b]	Fo (1)	Understory	no	Night (1)
Gryllidae	Podoscirtinae	*Calscirtus amoa*[b]	Fo (1)	Understory	?	Night (1)
Gryllidae	Podoscirtinae	*Calscirtus magnus*[b]	Fo (1)	Canopy	yes	Night (1)
Gryllidae	Podoscirtinae	*Matuanus affinis mirabilis*[b]	Fo (2)	Trunk	yes	Night (2)
Gryllidae	Podoscirtinae	*Pixipterus punctulatus*[d]	Sh (1)	Understory	no	Night (1)
Mogoplistidae	Mogoplistinae	*Mogoplistidae sp1*	Pr (2) / Sh (1)	Leaf litter/trunk	yes	Night (3)
Mogoplistidae	Mogoplistinae	*Mogoplistidae sp2*	Pr (4) / Sh (2)	Leaf litter/trunk/ understory	yes	Day (1) / Night (5)
Mogoplistidae	Mogoplistinae	*Mogoplistidae sp3*[d]	Sh (6)	Leaf litter/ understory	yes	Day (2) /Night (4)
Mogoplistidae	Mogoplistinae	*Mogoplistidae sp7*[b]	Fo (9)	Understory	yes	Day (1) / Night (8)
Phalangopsidae	Paragryllinae	*Protathra nana*[b]	Fo (1)	Trunks	yes	Night (1)
Phalangopsidae	Paragryllinae	*Caltathra balmessae*	Fo (2) / Pr (2)	Trunks/roots	no	Night (4)
Phalangopsidae	Paragryllinae	*Caltathra meunieri*	Fo (13) / Pr (2)	Trunks/roots	no	Day (1) / Night (14)
Phalangopsidae	Phaloriinae	*Pseudotrigonidium ana*	Fo (3) / Pr (5)	Trunks/leaf litter	no	Day (1) / Night (7)
Phalangopsidae	Phaloriinae	*Pseudotrigonidium caledonica*[b]	Fo (1)	Leaf litter/ understory	yes	Day (1)
Trigonidiidae	Nemobiinae	*Kanakinemobius sp*[b]	Fo (3) / Pr (1)	Understory	no	Night (4)
Trigonidiidae	Nemobiinae	*Koghiella flammea*	Pr (3) / Sh (116)	Leaf litter	yes	Day (59) /Night (60)
Trigonidiidae	Nemobiinae	*Koghiella nigris*	Fo (53) / Pr (8)	Bare soil	yes	Day (23) /Night (38)
Trigonidiidae	Nemobiinae	*Bullita fusca*	Fo (182) / Pr (98)	Leaf litter	yes	Day (128) / Night (152)
Trigonidiidae	Nemobiinae	*Bullita mouirangensis*[b]	Fo (21)	Leaf litter	yes	Day (12) / Night (9)
Trigonidiidae	Nemobiinae	*Bullita obscura*[c]	Pr (72)	Leaf litter	yes	Day (37) / Night (35)
Trigonidiidae	Nemobiinae	*Paniella bipunctatus*[b]	Fo (1)	Trunks	no	Day (1)
Trigonidiidae	Trigonidiinae	sp	Pr (1)	Leaf litter	?	Night (1)

Note: N/A indicates data not available.

[a] Number of specimens collected.

[b] Species unique to forest.

[c] Species unique to preforest.

[d] Species unique to shrubland.

while preforest and shrublands shared four. Forest and shrubland, however, shared no species.

Collected species additionally provided several unique characteristics. For instance, 70% of the cricket species collected were stridulatory species (Anso, Jourdan, & Desutter-Grandcolas, 2016). It was also found that forests contained the lowest percentage of acoustic species when compared to total species richness (65%), followed by shrublands (71.4%) and preforest (78.6%) (Table 2). Of all species collected, a total of eleven were collected only once during the entire taxonomic inventory. During this inventory, a larger number of species were collected at night (90%) than during the day (60%).

3.2 | Environmental succession

Environmental results demonstrated: (1) a clear difference in vegetation and climatic parameters between ecological stages, with a higher variability between shrubland and forested sites, and (2) a progression in the variable values that follow the ecological stage succession (Table 3).

A large number of vegetation parameters separated open shrublands from preforest and forest stages: a higher bare ground layer, a lower vegetation height, a lower number and size of stems, and a higher canopy openness. Conversely, vegetation parameters were identical between preforest and forest, with the exception of vegetation height, which was higher in the forest. The herbaceous layer and tree layer thus differed between forest and shrubland only. Plant species richness did not significantly differ when compared among ecological stages.

Several climatic parameters differed in the succession. Mean and maximum temperature, along with daily variation, followed the ecological gradient, (i.e., the highest and lowest values for shrubland and forests, respectively). Mean and minimum relative humidity differed significantly between forest and the two other ecological stages, with lowest and highest values for shrublands and forests, respectively. Daily humidity variation followed the ecological gradient (i.e., highest in shrublands, followed by preforest and subsequently forest). The minimum temperature and the maximum humidity were not significantly different between the successional stages.

3.3 | Alpha diversity of cricket assemblages

Species richness of crickets was not significantly different between sites of differing ecological stages due to large standard deviation values. This was indicative of a high variation of intra-site species richness values. However, the overall abundance of crickets was significantly lower in shrubland than preforest and forest (Table 3).

3.4 | Beta diversity of cricket assemblages

Each ecological stage showed clearly separated cricket assemblages (Figure 2) based on NMDS ordination (stress = 0.065, two dimensions). Thirteen environmental variables significantly contributed to the ordination model, with six at a high significance level ($p <= .01$): maximum temperature, daily temperature variation, mean temperature, percentage of canopy openness, vegetation height, and percentage of bare ground (Figure 2a). Cricket assemblages in shrubland were the most distinct, with a habitat characterized by an open canopy, a high percentage of bare ground coverage, and a large percentage of herbaceous and shrub growth. Cricket assemblages in forest and preforest were similar, with habitats characterized by a high canopy height, a high number of stems with a large circumference, and a high percentage of trees. These ecological stages explained 52% of the total variation in cricket assemblages observed from the taxonomic inventory (permutation test: $R^2 = 0.522$; $p = .004$). Similar results were obtained when considering the presence or absence of the cricket species (55%; permutation test: $R^2 = 0.551$; $p = .001$). Notably, the daily humidity significantly contributed to the ordination model (Figure 2b).

Focusing only on cricket species with a stridulatory apparatus produced similar results (Figure 2c). The ecological stages explained 53% of the total variation of the cricket assemblages (permutation test: $R^2 = 0.527$, $p = .006$). NMDS showed a clear succession of cricket assemblages along the ecological succession (stress = 0.034, two dimensions). Eleven environmental variables significantly contributed to the ordination model with a high significance for vegetation height and mean temperature ($p <= .01$). Considering the presence or absence of the cricket species, the ecological stages explained 60% of the total variation of the cricket assemblages (permutation test: $R^2 = 0.6$, $p = .001$). For that dataset, thirteen significant variables were identified for the ordination model, with seven of high significance ($p <= .01$): percentage of shrub layer, percentage of bare ground, vegetation height, percentage of canopy openness, maximum temperature, daily temperature variation, and daily humidity variation (Figure 2d).

Based on cricket assemblage spatial turnover and nestedness, results indicated that spatial turnover almost exclusively contributed to the beta diversity observed ($\beta = 0.874$, $\beta_{SIM} = 0.807$, $\beta_{NES} = 0.067$). The same analysis performed for the three ecological stages produced similar results ($\beta = 0.698$, $\beta_{SIM} = 0.567$, $\beta_{NES} = 0.131$). This suggests that species are replaced by others with low loss of species from other sites and ecological stages. Results from Section 3.3 that demonstrate a nonsignificant difference in species richness between sites of different ecological stages further support this idea.

3.5 | Relevant species by successional stage

SIMPER analysis demonstrated that specific cricket species were keys in distinguishing communities in the succession (Table 4), several of these species emitting specific calls making them a good candidate for being bioindicators detected by acoustic sensors. Based on species abundance in the assemblages, *Agnotecous azurensis*, *Koghiella flammea*, *Bullita fusca*, and *B. obscura* Anso & Desutter-Grandcolas,

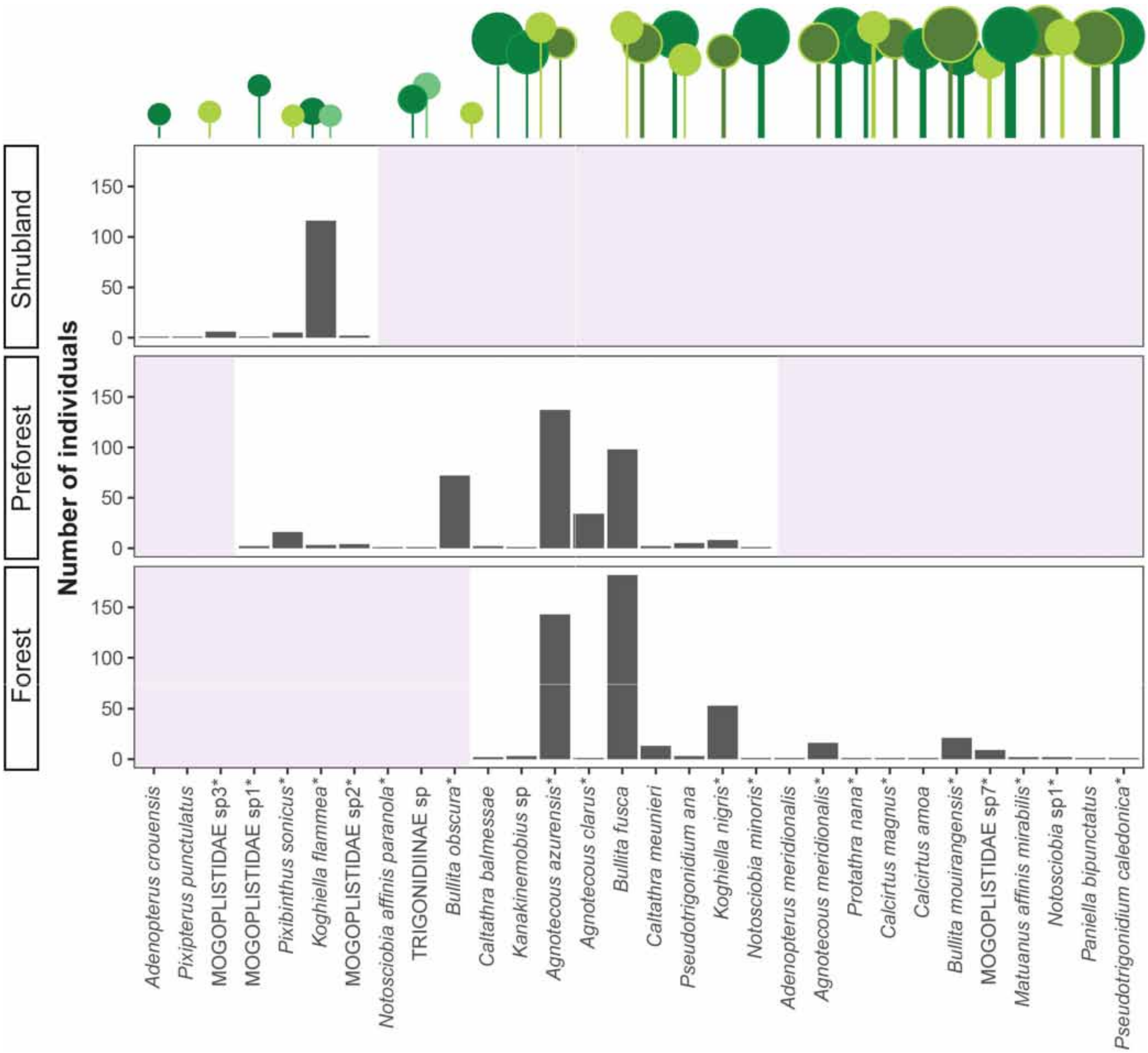

FIGURE 1 Cricket species assemblages along the ecological succession. * indicates stridulatory species.

2016 contributed the most to the differences between shrubland and preforest stages. These species live in leaf litter, with the ability to produce a species-specific calling song. *K. flammea*, *B. fusca*, and *B. obscura* are active by day, while *A. azurensis* species is active by night. Considering the differences between shrubland and forest stages, three species were found to contribute the most: *B. fusca*, *A. azurensis*, and *K. flammea*. Finally, *B. fusca*, *A. azurensis*, *B. obscura*, *and K. nigris* Anso & Desutter-Grandcolas, 2016 contributed the most to the differences between forest and preforest stages. *K. nigris* is a small nocturnal Nemobiinae (Trigonidiidae) living strictly in forested habitat, in a peculiar microhabitat (i.e., bareground).

Applying this analysis to the species presence or absence in the assemblages resulted in a larger number of contributing species (Table 5). The species contributing the most to the differences between preforests and shrublands were *A. clarus* Desutter-Grandcolas, 2006, and *K. flammea*. *A. clarus* is acoustically active by night and collected on three preforest sites versus once in forest sites. Differences between forests and shrublands were mainly associated with *A. azurensis*, *Caltathra meurieri* Anso & Desutter-Grandcolas, 2016, and *K. flammea*. *C. meunieri* is a nocturnal Phalangopsidae living on large trunks or roots, without stridulatory apparatus (i.e., "mute species") and found in every forest site but only at two preforest sites. The two species *A. clarus* and *C. meurieri* were found to contribute the most to the difference between preforests and forests.

4 | DISCUSSION

The results of this study highlight the central role of crickets in conservation biology and demonstrate that crickets could be relevant bioindicators of the restoration process and integrity of the environment in tropical systems.

TABLE 3 Mean values (± standard deviation) of cricket assemblages, vegetation attributes, and climatic parameters in the three ecological stages calculated from values averaged per sites. P represents the significance of the values after post hoc Kruskal–Wallis tests according to Conover for pairwise multiple comparisons of the ranked data between stages

	Shrubland	Preforest	Forest	*P*
Cricket assemblage				
Species richness	3.5 ± 1.29	7 ± 2.71	7.5 ± 3.7	-
Overall abundance	16.5 ± 9.58	48.38 ± 15.19	57.13 ± 12.85	Fo-Sh**, Pr-Sh*
Vegetation attributes				
Herbaceous layer (%)	55.4 ± 24.1	23.8 ± 16.5	12.5 ± 13.4	Fo-Sh*
Shrub layer (%)	53.8 ± 13.8	31.2 ± 8.3	32.8 ± 12.1	-
Tree layer (%)	2.5 ± 2	37.2 ± 17.5	35.3 ± 8.6	Fo-Sh*
Bare ground (%)	27.5 ± 11.5	0.6 ± 1.3	0 ± 0	Fo-Sh***, Pr-Sh***
Vegetation height (m)	2.25 ± 0.96	14.9 ± 2.25	23.8 ± 4.33	Fo-Sh***, Fo-Pr**, Pr-Sh**
Number of stems (n°.)	0.5 ± 0.71	19 ± 11.6	15.9 ± 5.19	Fo-Sh*, Pr-Sh*
DBH of stems (n°.)	12.6 ± 14.8	56 ± 11.6	57.5 ± 11.5	Fo-Sh*, Pr-Sh*
Canopy openness (%)	90.6 ± 6.7	9.81 ± 3.15	7.23 ± 0.75	Fo-Sh**, Pr-Sh*
Plant species richness	17.4 ± 2.43	14.8 ± 2.33	18.1 ± 6.02	-
Climatic parameters				
Mean temperature (°C)	21.5 ± 0.76	19.5 ± 0.53	18.6 ± 0.43	Fo-Sh***, Fo-Pr*, Pr-Sh*
Minimum temp. (°C)	16.2 ± 1.59	16.5 ± 0.97	16.6 ± 0.37	-
Maximum temp. (°C)	28.8 ± 2	24 ± 0.61	21.2 ± 0.71	Fo-Sh***, Fo-Pr**, Pr-Sh**
Daily temp. variation (°C)	12.6 ± 2.6	7.54 ± 1.26	4.65 ± 0.52	Fo-Sh***, Fo-Pr**, Pr-Sh**
Mean humidity (%)	78.5 ± 4.8	82.9 ± 1.5	88.1 ± 1.62	Fo-Sh**, Fo-Pr*
Minimum hum. (%)	47.4 ± 8.91	59.1 ± 1.54	68.8 ± 2.61	Fo-Sh***, Fo-Pr*
Maximum hum. (%)	96.1 ± 2.45	97 ± 1.35	96.4 ± 1.28	-
Daily hum. variation (%)	48.8 ± 6.51	37.9 ± 1.34	27.6 ± 1.39	Fo-Sh***, Fo-Pr**, Pr-Sh**

*$p < .05$; **$p < .01$; ***$p < .001$; Fo signifies Forest, Pr Preforest, and Sh Shrubland.

4.1 | Cricket assemblages along ecological succession

Cricket assemblages clearly responded to the different stages along the environmental gradient, with several distinct species in each stage. Overall cricket abundances were highest in forested habitats (i.e., forest and preforest), suggesting that these habitats provide the best trade-off between food resources (Barberena-Arias & Aide, 2003; Williams et al., 2008), shelter from predators (Brouwers & Newton, 2009), and favorable moisture conditions. Oviposition sites may also be more important and various in forested habitats than in more open ones. This is especially important for litter-dwelling species, explaining higher densities in closed habitats (Huber, 1989). These results are similar to those obtained for forest-dwelling grasshoppers in Western Amazonia by Amédégnato and Descamps (1980). Lower cricket densities in shrublands might be explained by smaller optimal vegetation patches, but also warmer mean and high temperatures, lower relative humidity, and limited food resources (Shik & Kaspari, 2010). Moreover, in drier habitats, such as shrublands, cricket density may be further constrained by higher predation rates in combination with limited shelter (McCluney & Sabo, 2009, 2014).

Accumulated species richness similarly showed a pattern related to ecological succession, with the highest number of species found in forested habitats (forest and preforest). This presumably reflected greater habitat complexity and microhabitat availability (Shik & Kaspari, 2010). However, based on the number of species found at each site, the differences were not significant between ecological stages. This could mean that a larger number of sites is needed to fully describe the cricket assemblages living in forests as compared to preforests or shrublands. Although preforest and forest share a large number of cricket species, the latter is characterized by a higher percentage of unique species. This pattern is expected for rich forest ecosystems (Rahman et al., 2012) and comparable with fruit-feeding butterflies, birds, leaf litter amphibians, and the crickets documented in Brazilian forests (Barlow et al., 2007; Szinwelski et al., 2012). While habitat complexity and heterogeneity might explain higher species richness in forests (Shik & Kaspari, 2010), they were surprisingly close to preforests in their vegetation attributes; however, they were clearly different in climatic conditions (i.e., temperature and relative humidity).

These observations highlight the importance of fine vegetation attributes or microhabitats (e.g., dead trunks, woody debris, and gaps around roots) along with microclimate condition (i.e., high moisture, low variation of temperature and humidity) in explaining community differences between these two advanced stages of forest regeneration, that are forest and preforest, in the southern part of New Caledonia. Among the ten species exclusively found in the forest, eight

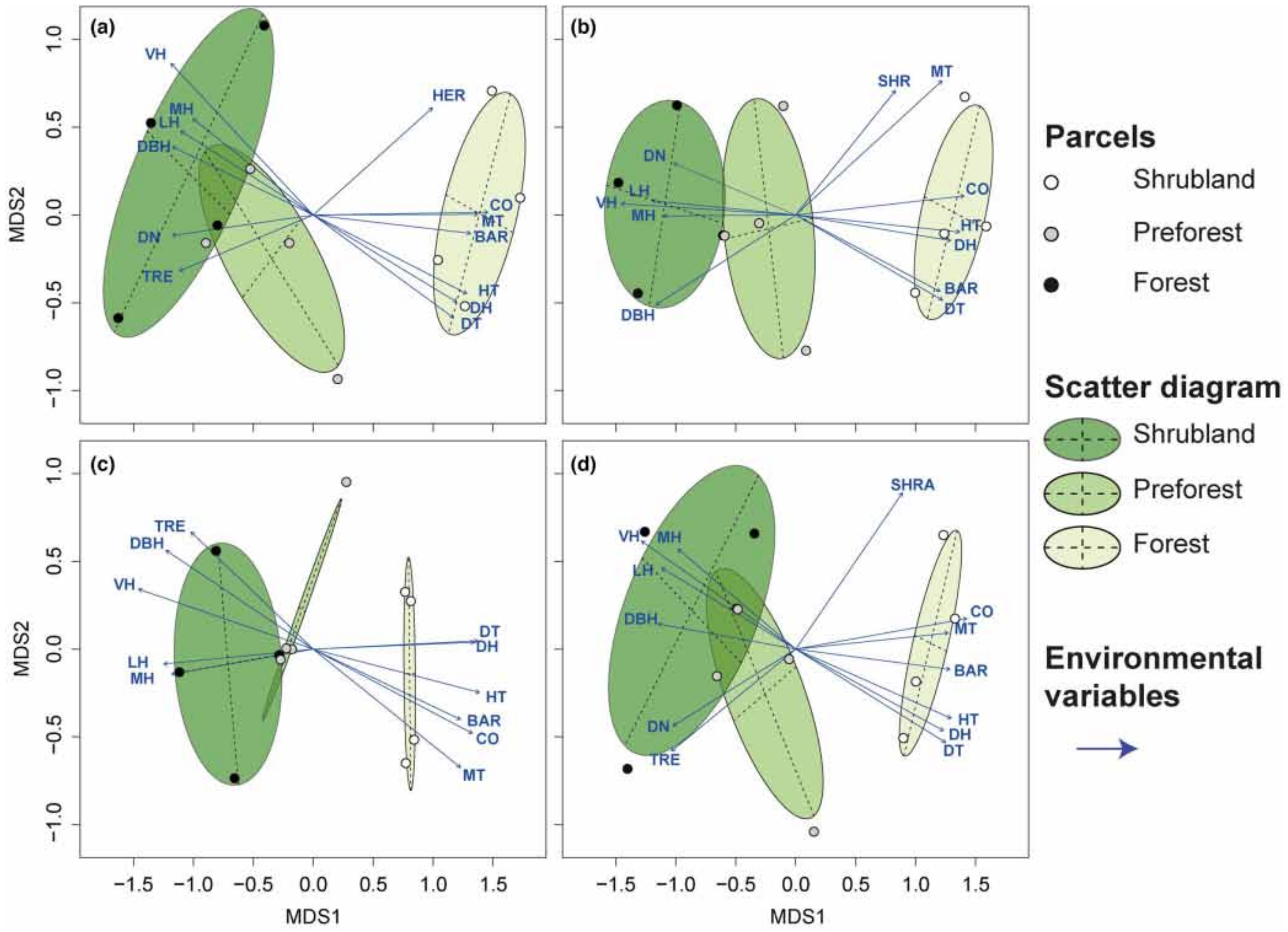

FIGURE 2 (a) NMDS based on cricket species abundances per site. (b) NMDS based on the presence or absence of cricket species per site. (c) NMDS based on abundances of soniferous cricket species per site. (d) NMDS based on the presence and absence of soniferous cricket species per site. Scatter diagrams (coefficient for the inertia ellipse size = 1.5) were drawn according to the habitat type. Significant fitted environmental variables are shown with the following abbreviations: HER for herbaceous layer, SHR for shrub layer, TRE for tree layer, BAR for bare ground, VH for vegetation height, DN for number of stems, DBH for number and diameter of stems, CO for canopy openness, MT for mean temperature, HT for maximum temperature, DT for daily temperature variation, MH for mean humidity, LH for minimum humidity, and DH for daily humidity variation.

TABLE 4 Contribution percentage of the most influential species for each pair of habitats calculated based on species abundances, with cumulative percentages in parentheses. The most influential species have with a minimum cumulative percentage of 70% of the contributions

	Forest		Shrubland	
Preforest	*Bullita fusca*	28% (28%)	*Agnotecous azurensis*	28% (28%)
	Agnotecous azurensis	17% (45%)	*Koghiella flammea*	22% (50%)
	Bullita obscura	15% (60%)	*Bullita fusca*	19% (69%)
	Koghiella nigris	11% (71%)	*Bullita obscura*	14% (83%)
Shrubland	*Bullita fusca*	29% (29%)		
	Agnotecous azurensis	26% (55%)		
	Koghiella flammea	19% (74%)		

were found on vegetation strata, interestingly suggesting a close relationship to vegetation attributes (i.e., plant species or structure), and likely further interrelated with the older age of forest habitat.

Some cricket species were previously described as potential indicator of an ecological stage such as *Pseudotrigonidium caledonica*, previously described as inhabiting forest understory and singing on low vegetation with a unique and recognizable low-frequency song (Desutter-Grandcolas et al. Desutter-grandcolas et al., 2016). However, the statistical analyses presented in this paper did not reveal *Pseudotrigonidium caledonica* (Otte, 1987) to be a significant

TABLE 5 Contribution percentage of the most influential species for each pair of habitats calculated based on presence of the species, with cumulative percentages in parentheses. The most influential species have with a minimum cumulative percentage of 70% of the contributions

	Forest		Shrubland	
Preforest	*Agnotecous clarus*	9% (9%)	*Agnotecous clarus*	11% (11%)
	Caltathra meunieri	7% (16%)	*Koghiella flammea*	10% (21%)
	Pseudotrigonidium ana	6% (22%)	*Agnotecous azurensis*	8% (29%)
	Koghiella nigris	6% (28%)	*Bullita fusca*	8% (37%)
	MOGOPLISTIDAE sp2	5% (33%)	MOGOPLISTIDAE sp3	8% (45%)
	Bullita fusca	6% (39%)	*Pseudotrigonidium ana*	8% (53%)
	Bullita mouirangensis	4% (43%)	MOGOPLISTIDAE sp2	6% (59%)
	Kanakinemobius sp	4% (47%)	*Pixibinthus sonicus*	5% (64%)
	Caltathra balmessae	3% (50%)	*Caltathra meunieri*	6% (70%)
	Notosciobia minoris	4% (54%)		
	Pixibinthus sonicus	4% (58%)		
	TRIGONIDIINAE sp	3% (61%)		
	Agnotecous azurensis	3% (64%)		
	Bullita obscura	4% (68%)		
	MOGOPLISTIDAE sp1	3% (71%)		
Shrubland	*Agnotecous azurensis*	10% (10%)		
	Caltathra meunieri	10% (20%)		
	Koghiella flammea	11% (31%)		
	MOGOPLISTIDAE sp3	7% (38%)		
	Bullita fusca	4% (44%)		
	MOGOPLISTIDAE sp2	5% (49%)		
	Pixibinthus sonicus	4% (53%)		
	Pseudotrigonidium ana	5% (58%)		
	Koghiella nigris	4% (62%)		
	Bullita mouirangensis	4% (66%)		
	Adenopterus crouensis	4% (70%)		

indicator of the forest. This is due to the fact that this species was collected only once in our survey, which highlights an important bias of our analyses towards rare species.

Previously, Desutter-Grandcolas (1997) have described the cricket community in New Caledonia forested habitat for different soil types (volcano-sedimentary rocks) than those studied here (ultramafic soil). Their cricket community structure was described as close to our forest community (in terms of species richness and dominant species), with 23 species identified belonging to the same genera, but all different at the species level. Taken together, the studies seem to confirm cricket genera specialization for habitats of a given vegetation type and plant structure (Anso, Jourdan, & Desutter-Grandcolas, 2016) and the microendemism pattern of Orthoptera species in New Caledonia (Grandcolas et al., 2008).

4.2 | Implications for conservation

The findings presented here provide strong evidence that cricket species and their assemblages are sensitive indicators of ecological succession in New Caledonia, with potential for applications in conservation. There are several characteristics that make them highly suitable as bioindicators for terrestrial monitoring in New Caledonia. In combination with the bioindicator evaluation by Gerlach et al. (2013), New Caledonian crickets are found in high densities throughout the year, can be easily sampled by sight or hearing, are sensitive to ecological stresses, and have a thorough taxonomic understanding including various ranges of bioclimatic preferences (Desutter-Grandcolas, 1997; Desutter-grandcolas et al., 2016; Otte et al., 1987). Available data on assemblages of crickets in scientific literature tend to show that crickets could be good bioindicators in other tropical areas, as they are most diverse in the tropics, especially in forested habitats. This reinforces the use of Orthoptera as bioindicators (Gerlach et al., 2013).

All the ecological stages considered in this study are important for conservation as each harbors a distinctive assemblage of cricket species and their destruction would lead to irreversible loss of unique biodiversity in New Caledonia. This provides valuable insight for managers and decision-makers and further highlights the large biodiversity of New Caledonian forests, with numerous endemic genera and species.

Open shrublands are usually less studied for their fauna (Chazeau, 1993) as they are often defined as the result of ecological degradation by human activities. While this description may be apt for particularly degraded areas, shrublands can be valuable for conservation efforts. In the present study, open shrubland harbored several distinct species and genera inhabiting leaf litter and shrubs. Some species are particularly useful in capturing the impact of specific disturbances (i.e., fires, climatic oscillations) demonstrating the different level of disturbances throughout the shrubland possibilities. This was demonstrated with the discovery of the new monotypic genus *Pixibinthus* Robillard & Anso 2016 in open shrubland and some preforest that provided useful information about fire regimes and climatic fluctuations and their subsequent influences on historic diversification processes in New Caledonia (Anso, Barrabé, et al., 2016). While high species richness has long been established in New Caledonian shrublands for plants, their value for animal conservation is here highlighted. As gallery forests in the Neotropical region, shrublands are not only “forests-to-be” that serve as corridors for forest species but host an original fauna of their own.

4.3 | Recommendations and perspectives for passive acoustic monitoring

The sampling design is highly important when studying crickets. Previous research on the response of cricket communities to vegetation succession has shown contrary or inconclusive results; however, this could be due to a lack of taxonomic expertise, inadequate sampling methodology, and/or the type of habitat (nontropical areas or grasslands for example are usually poor in cricket species). For example, while Araújo et al. (2015) found no relationship between habitat degradation (from highly degraded to natural forested habitats) and cricket abundances, the passive trapping system (i.e., pitfall trap) used was not adequate to sample cricket communities (Gardiner et al., 2005), potentially leading to bias in the results. Because numerous cricket species live on vegetation, rocks, or tree trunks, with restricted displacements on leaf litter (Desutter-Grandcolas, 1992, 2002; Jain & Balakrishnan, 2011), the low abundances of crickets obtained by Araújo et al. (2015) (3–5 individuals per habitat) cannot be considered a sufficient evaluation of cricket communities. Similarly, there are several other studies that were inconclusive for crickets because of the low species richness recorded in nontropical steppes or meadows (Fartmann et al., 2012; Marini et al., 2009).

When adequate sampling and taxonomic effort are present, crickets are a powerful tool to evaluate the effect of succession on insect communities in the tropics. The most comprehensive study to date for cricket communities was conducted along a large forest regeneration gradient in Brazil (i.e., in a 300-year time period) (Szinwelski et al., 2012). Positive correlations between species richness and forest age, canopy cover, and litter depth was a key finding. Critically, Szinwelski et al. (2012) provided strong evidence of cricket species succession and specificity along a large habitat chronosequence, including open to closed habitats, with a comparable turnover in species composition to our results in New Caledonia. Similar results were obtained for a forest succession over 250 years in Western Amazonia, where different cricket communities were found in the forest plots according to their age of regeneration after slash-and-burn cultivation (Desutter, 1990).

This work is part of a larger research program about Neocaledonian crickets and contributes to highlight the potential value of crickets as an environmental indicator of tropical ecosystems. It further provides a unique opportunity for Passive Acoustic Monitoring (PAM).

Firstly, New Caledonian cricket fauna comprises many acoustically active species. In the present work, of the 30 species inventoried, 20 can produce sound, i.e., 67%. For comparison, among the 23 species collected by Desutter-Grandcolas (1997), 14 (= 61%) can stridulate. Based on those two studies, bioacoustics may capture up to two-thirds of cricket species in New Caledonia. Secondly, calling songs are composed of a stereotyped repetition of syllables (sensu Ragge & Reynolds, 1998) with a narrow carrier frequency, and both the frequency spectrum and the call temporal pattern allow for highly reliable species identifications (Diwakar & Balakrishnan, 2007; Jain et al., 2014; Riede, 1997). Thirdly, cricket calls are abundant and dominate the neocaledonian soundscapes, particularly at night, whether it be in shrubland, preforest, or forest (Gasc et al., 2018). Thereby, Gasc et al. (2018) concluded that only 6 days of passive acoustic recordings were necessary to describe the calling cricket community. Fourthly, calling cricket communities reliable bioindicators of the surrounding environment and their analyses can reveal major environmental perturbation. In the present work, community analysis was performed only with stridulating crickets revealing the same succession-based specialization as compared to the analyses using all species. As shown by Gasc et al. (2018), the presence of the invasive ant *Wasmannia auropunctata* resulted in a significant reduction in cricket species and their acoustic activity.

In contrast with other methods, such as fogging or traditional taxonomic inventories, the ecoacoustic approach is advantageous as it is noninvasive, easy to implement, allow data collection over large temporal and spatial scales, and in remote places (Sueur & Farina, 2015). An acoustic approach for biodiversity monitoring is meaningful in species-rich ecosystems, such as tropical rainforests (Deichmann et al., 2018), where taxonomic impediments may be overcome by the recognizable taxonomic unit of songs (Riede, 1998, 2018). Acoustic monitoring could not, however, be used to characterize the sampled communities by their specific components unless a preliminary taxonomic effort was conducted. When possible, taxonomic inventory to establish ground knowledge combined with passive acoustic monitoring to sample natural environments seems an effective strategy, and especially necessary in the tropics where biodiversity still needs description. The research effort in ecoacoustics conducted the last decade in New Caledonia within the same research program, including the present work, brought together sufficient taxonomic, ecoacoustic, and ecological knowledge to confirm the value of crickets as bioindicators and support the use of a passive acoustic approach to monitor ecosystems (Anso, Jourdan, & Desutter-Grandcolas, 2016; Gasc et al., 2013, 2018). Because crickets are globally distributed, particularly in endangered biodiversity hotspots and in the tropics, they can be a key tool and metric for conservation programs.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.2280gb5w3 (Anso et al., 2022) and https://github.com/agasc/Anso-et-al-2022-Biotropica.

ORCID

Amandine Gasc https://orcid.org/0000-0001-8369-4930
Laure Desutter-Grandcolas https://orcid.org/0000-0002-7781-3451
Hervé Jourdan https://orcid.org/0000-0002-3756-4008

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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