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Herve Jourdan, Edouard Bourguet, Christian Mille, Roman Gula, Jörn Theuerkauf

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Impact of invasive little fire ants *Wasmannia auropunctata* on rainforest soil fauna: implications for conservation of the endangered flightless kagu of New Caledonia

Hervé Jourdan · Edouard Bourguet ·
Christian Mille · Roman Gula ·
Jörn Theuerkauf

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Abstract The little fire ant, *Wasmannia auropunctata*, is an invasive species known to negatively affect many native species in its introduced range. Here, we studied the effect of little fire ant presence on the biomass of soil fauna in rainforest of New Caledonia to assess if little fire ants have an impact on an endangered endemic flightless bird, the kagu, *Rhynochetos jubatus*. The average biomass of soil fauna (except for millipedes) was lower in 53 sample plots with little fire ants than in 597 sample plots without little fire ants and the biomass decreased with increasing density of little fire ant nests. Millipedes on the contrary seemed to be positively impacted as their average biomass was higher in areas with fire ants than in areas without, but even millipede biomass decreased with increasing nest density of fire ants. Kagu density decreased with increasing area of rainforest invaded

by little fire ants, suggesting, given their observed negative impact on soil fauna biomass, that they may limit food resources for kagu. Little fire ants might therefore transform rainforest into a less suitable habitat for the kagu by reducing the biomass of their prey and thus have a negative impact for kagu conservation.

Keywords *Wasmannia auropunctata* · Indirect impact · Invasive ant · Soil fauna

Ants are one of the most ecologically successful and numerically dominant insect groups, especially in tropical terrestrial ecosystems, in which they play key roles as predators, saprophages, nutrient recyclers, soil engineers and regulators of plant growth and reproduction (Del Toro et al. 2012). Nonetheless, some ants are known as highly invasive species that interfere with many components of ecosystems (Holway et al. 2002; Clarke et al. 2021). The little fire ant, *Wasmannia auropunctata*, is considered as one of the worst invasive ant species (Jourdan 1997; Dunham and Mikheyev 2010; Vonshak et al. 2010), threatening native ants (Le Breton et al. 2003; Walker 2006; Bertelsmeier et al. 2015), crickets (Gasc et al. 2018; Anso et al. 2022), lizards (Jourdan et al. 2001), and even mammals (Walsh et al. 2004). Little fire ants are expected to also threaten other taxonomic groups (Lubin 1984; Duham and Mikheyev 2010; Anso et al. 2022) and to promote sap-sucking insects (Le Breton

H. Jourdan · E. Bourguet
Aix Marseille Univ, Univ Avignon, CNRS, IRD, IMBE
(Institut Méditerranéen de Biodiversité et d'Ecologie
Marine et Continentale), IRD Nouméa, BP A5,
98848 Nouméa Cedex, New Caledonia

C. Mille
Institut Agronomique Néocalédonien (IAC), Équipe
ARBOREAL, Station de Recherche Agronomique de
Pocquereux, Laboratoire d'Entomologie Appliquée, BP
32, 98880 La Foa, New Caledonia

R. Gula · J. Theuerkauf (✉)
Museum and Institute of Zoology, Polish Academy
of Sciences, Wilcza 64, 00-679 Warsaw, Poland
e-mail: jtheuer@miiz.eu

et al. 2005), but there has not yet been a comprehensive study of their impact on the entire soil fauna.

Little fire ants were unintentionally introduced to New Caledonia in the early 1960s and began spreading throughout the islands of the whole archipelago across most habitats including native rainforest (Jourdan 1997; Le Breton et al. 2003). As the species lacks an efficient nuptial flight and has clonal reproduction (Fournier et al. 2005), it has mainly been spread by human activity (Walsh et al. 2004). In New Caledonia, it has been spread by soil or firewood to rainforest reserves, in which their further colonisation speed is about 10–20 m per year (H. Jourdan, unpublished data). Since the introduction of little fire ants, research in New Caledonia has focussed on their biology (Jourdan 1997, 1999; Jourdan et al. 2001; Le Breton et al. 2003, 2004, 2005). Here, we use data collected during the study of an endangered flightless bird, the kagu, *Rhynochetos jubatus* (Eurypygiiformes: Rhynochetidae). The kagu is the only species of its family, the only extant flightless bird of New Caledonia, and unique also due to its complex social organisation otherwise found only in human societies (Theuerkauf et al. 2018). We aim at demonstrating that little fire ants not only threaten other ant species but also change the soil fauna composition in general and potentially transform rainforest into a less suitable habitat for the kagu by reducing the biomass of their prey. This degradation of habitat may have severe conservation impacts for the kagu as human colonisation of New Caledonia 3000 years ago already drove kagu into suboptimal habitats and caused an about 30% reduction in body mass (Theuerkauf and Gula 2018). The focus in our kagu study was assessing food abundance in sample plots within home ranges of 34 kagu families in two protected sites of New Caledonia, which represent poor and productive kagu habitats (Theuerkauf et al. 2017). As the food of kagu includes nearly the whole soil fauna larger than about 5 mm of length (with the exception of ants and mites, authors' unpublished data of cafeteria tests), our sampling design allowed us to also directly assess the impact of little fire ants on the soil fauna.

We conducted our research in two protected areas, the *Parc Provincial de la Rivière Bleue* (PPRB, 22°3–12'S, 166°33–46'E), to which little fire ants were introduced around 1997, and the *Parc Provincial des Grandes Fougères* (PPGF, 21°30–39'S,

165°39–50'E), to which the species was introduced around 1984. The PPRB is a 221-km² reserve on ultramafic soils with a mean annual rainfall of about 2900 mm and mean annual temperature of 21 °C. Ultramafic soils are extremely low productive and rich in heavy metals. We worked in rainforests at altitudes of 150–350 m asl. The PPGF is a 45-km² reserve on oligotrophic schist soils, with a mean annual rainfall of about 1,600 mm and a mean annual temperature of 20 °C. We worked in rainforests at altitudes of 300–500 m asl.

To ensure that the sample plots were representative for each kagu family, we predefined straight transects dissecting the family's home range and spaced sample plots at 25-m distances along the transect. From 2008 to 2021, we assessed the abundance of soil fauna larger than about 5 mm in 650 sample plots of 1 m² (delimited by a 1 m × 1 m frame) by hand inspecting the entire litter transferred to white plastic bowls during the hot wet season (December to April, n = 120 sample plots), the cool wet season (April to August, n = 170) and the warm dry season (August to December, n = 370). Little fire ants were present in 10% of sample plots in the ultramafic site (n = 310) and 6.5% of sample plots in the non-ultramafic site (n = 340). The sample plots were distributed representatively, so these proportions correspond approximately to the area colonised by little fire ants in each study site.

Because there were seasonal differences in soil fauna abundance (Fig. 1a), we normalised biomass with seasonal correction factors. We calculated seasonal correction factors for each study site separately as the average abundance over the whole year divided by the average abundance in a given season. During inspection of sample plots, we counted the number of individuals in each taxonomic order to assess abundance. We weighed some of the captured individuals alive with electronic scales to the next 0.001 g and calculated average mass of an individual for each order (Table 1). We then calculated biomass of individual sample plots as the sum of products of average mass and number of individuals in each order. We estimated home ranges of the 34 kagu families as 100% Minimum Convex Polygons (MCP) of locations taken during our kagu radio-tracking study (Theuerkauf et al. 2018). We then calculated density as the number of kagu in a family divided by the home range size. Because our two study sites were of different productivity resulting in different kagu

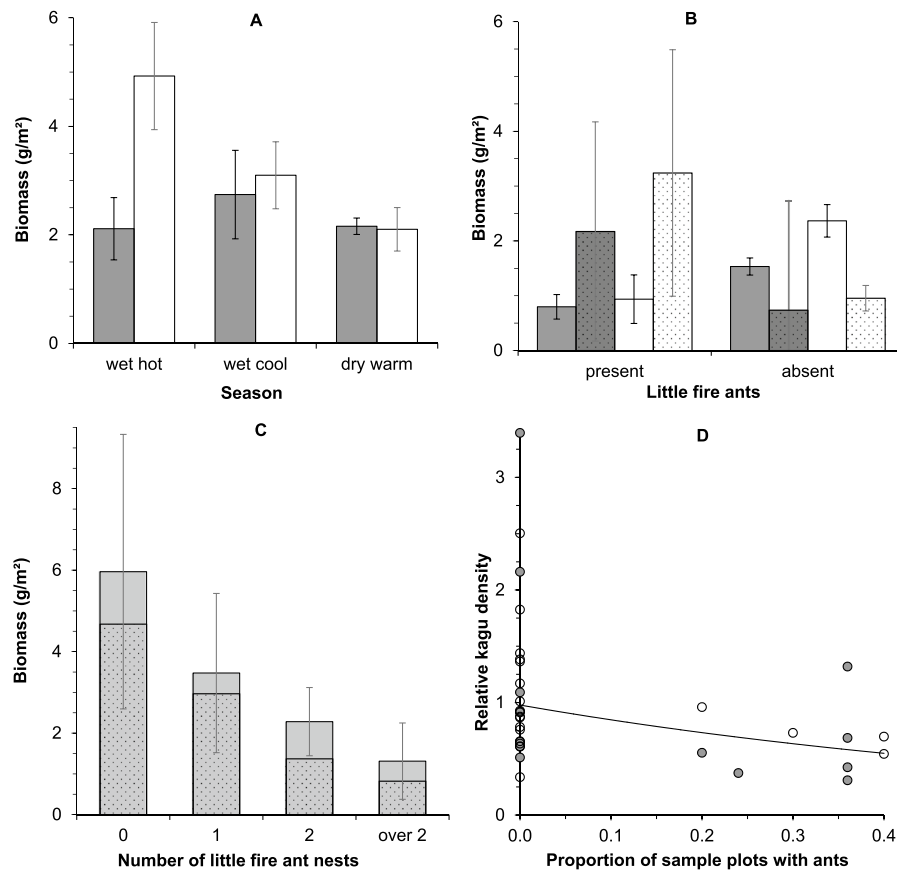


Fig. 1 Average (with 95% confidence intervals) biomass of soil fauna (A) in sample plots during the wet hot ($n=120$), the wet cool ($n=170$) and the dry warm ($n=370$) season in the ultramafic study site (grey bars) and the non-ultramafic study site (white bars), (B) seasonally normalised biomass of Julida (dotted bars) and non-Julida soil fauna in sample plots with little fire ant presence ($n=53$) and absence ($n=597$) in the ultramafic (grey bars) and the non-ultramafic study site (white bars), (C) seasonally normalised biomass of all soil

fauna in relation to the number of little fire ant nests (dotted area represents the proportion of Julida) on sample plots colonised by fire ants ($n=53$), and (D) exponential regression ($y=0.978e^{-1.452x}$, $F=6.213$, $R^2=0.163$, $P=0.018$) between the proportion of sample plots with little fire ants and relative kagu density (proportion of average in the respective study site) of 34 kagu families in the ultramafic (grey circles) and the non-ultramafic site (white circles)

density, we standardised kagu density by dividing the density of each family by the average kagu density in the respective study site.

In both study sites, the biomass of soil fauna (except for Julida) was at least twice as high in sample plots without little fire ants than in sample plots with little fire ants (Fig. 1b, Table 1) and the biomass decreased with increasing nest density of little fire ants (Fig. 1c). Phasmatodea, Orthoptera, Blattodea, Haplotaaxida, Araneae and Amphipoda appeared to be the most negatively impacted by the presence of ants (Fig. 2). Julida on the contrary seemed to be positively impacted as their biomass was higher in

areas with fire ants than in areas without (Figs. 1b, 2, Table 1). However, with increasing densities of little fire ant nests, Julida numbers started decreasing as well (Fig. 1c). There appeared to be a trend for lower relative kagu density with an increasing proportion of the home range invaded by little fire ants (Fig. 1d).

Most of the documented effects of invasive ants on native invertebrate species are direct predation or competition for reproductive sites (Holway et al. 2002). Due to the high abundances that invasive ants can achieve, they can cause population declines or local extinctions of invertebrates (Clarke et al. 2021). We demonstrated an important difference in the

Table 1 Average live mass (with confidence interval) and sample size (n) of weighed individuals belonging to different taxonomic orders of soil fauna, total number of individuals in all 650 sample plots, and average biomass (with confidence interval) per order, calculated as the product of average

mass and number of individuals, for sample plots with little fire ant presence (n=53) and absence (n=597). Abundances with non-overlapping confidence intervals between plots with and without little fire ants are in bold (if number of individuals > 20)

Class	Order	Live mass (g)	n	Number of individuals	Biomass (g/m ²) with fire ants	Biomass (g/m ²) without fire ants
Clitellata	Haplotaxida	1.497 ± 0.479	36	294	0.113 ± 0.133	0.727 ± 0.150
Arachnida	Amblypygi	0.02	*	11	0	0.0004 ± 0.0002
	Araneae	0.106 ± 0.081	28	566	0.024 ± 0.013	0.098 ± 0.010
	Opiliones	0.059 ± 0.103	4	24	0.006 ± 0.005	0.002 ± 0.001
	Scorpiones	0.1	*	19	0.002 ± 0.004	0.003 ± 0.002
Malacostraca	Amphipoda	0.038 ± 0.017	31	4796	0.127 ± 0.062	0.297 ± 0.028
	Isopoda	0.086 ± 0.049	24	484	0.049 ± 0.024	0.066 ± 0.010
Entognatha	Diplura	0.001	*	4	0	0.00001 ± 0.00001
Insecta	Archeognatha	0.024 ± 0.006	3	14	0	0.0006 ± 0.0003
	Blattodea	0.109 ± 0.042	7	283	0.006 ± 0.009	0.051 ± 0.008
	Coleoptera	0.164 ± 0.094	38	289	0.109 ± 0.041	0.070 ± 0.022
	Dermaptera	0.059 ± 0.024	19	53	0.002 ± 0.003	0.005 ± 0.002
	Diptera larvae	0.124 ± 0.074	6	31	0.007 ± 0.010	0.006 ± 0.003
	Embioptera	0.002**	2	3	0	0.00001 ± 0.00001
	Hemiptera	0.172 ± 0.077	15	67	0.010 ± 0.011	0.018 ± 0.005
	Isoptera	0.013**	20	62	0	0.001 ± 0.001
	Lepidoptera larvae	0.307 ± 0.150	8	46	0.017 ± 0.019	0.022 ± 0.008
	Neuroptera larvae	0.1	*	4	0.002 ± 0.004	0.001 ± 0.001
	Orthoptera	0.298 ± 0.077	21	398	0.017 ± 0.019	0.197 ± 0.027
	Phasmatodea	0.107 ± 0.056	5	21	0	0.004 ± 0.002
	Chilopoda	Scolopendromorpha	0.267 ± 0.295	10	88	0.035 ± 0.025
Scutigermorpha		0.002	*	1	0	0.000003 ± 0.000007
Diplopoda	Julida	2.017 ± 0.591	52	295	2.283 ± 0.832	0.794 ± 0.137
Reptilia	Squamata	0.550 ± 0.043	11	32	0.010 ± 0.020	0.029 ± 0.010
Gastropoda	Pulmonata	0.962 ± 0.243	21	90	0.200 ± 0.128	0.127 ± 0.035
Rhabditophora	Tricladida	0.403 ± 0.128	9	105	0.061 ± 0.054	0.066 ± 0.020

*No samples for weighing, therefore estimated mass

**Individuals weighed together, therefore no confidence interval

composition of soil fauna in areas colonised by little fire ants and in areas without, which has also been observed in New Caledonian canopy fauna (Jourdan 1999). As there might be confounding environmental factors and we did not use an experimental design with little fire ant exclusion to prove changes (Kumschick et al. 2014), our results are no direct proof for changes caused by little fire ants. However, we think, given the relatively large sample size and the repetition in two sites, that our study provides sufficient indication for a probable effect of fire ants on soil fauna composition. This change in community

structure may even lead to cascading effects at higher trophic levels as pointed out by Jourdan et al. (2001) for endemic litter-dwelling skinks and some arboreal geckos. The negative effect on reptiles in our study was less obvious, probably because the most often observed reptiles were lizards of the genus *Nannoscincus*, which are burrowers and use the lower layer in the litter (Sadlier et al. 2014), whereas little fire ants use the upper layer for both foraging and nesting (Orivel et al. 2009). We might also have underestimated the negative effect if some lizards escaped the sample plots before we could spot them.

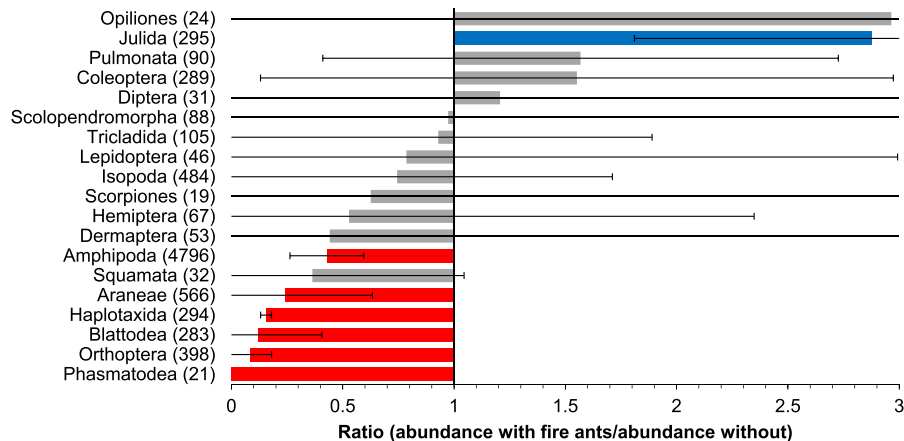


Fig. 2 Ratio (with confidence interval) of abundance in sample plots with little fire ants ($n=53$) divided by abundance in sample plots without little fire ants ($n=597$) for each order of soil fauna (in parentheses total number of individuals in all

plots). Negatively impacted orders in red (confidence interval entirely below 1), positively impacted in blue (confidence interval above 1) and neutral in grey (confidence interval including 1)

Our study demonstrates likely ant-associated declines in the abundance of various orders of soil fauna. This results in a decrease in soil fauna biomass that is somewhat mediated by the increase in *Julida* biomass. It is likely that the *Julida* biomass increase was caused by the suppression of other predators through little fire ants in early phases of the invasion. However, even *Julida* biomass decreased with increasing density of little fire ants, which in later phases of the invasion could lead to a reduction of food resources for *kagu*. The observed trend of higher relative *kagu* density in areas with a smaller proportion of area invaded by little fire ants indicates that the presence of the ants probably reduces resources for *kagu*. As the reproductive output of *kagu* is relative to resources (Theuerkauf et al. 2017), colonisation by little fire ants may indirectly limit *kagu* population growth and therefore may have a negative impact for *kagu* conservation as long as the little fire ants can maintain high abundance.

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Authors' contributions HJ, RG and JT contributed to the study conception and design. All authors contributed to data collection. HJ and JT performed data analysis and wrote the

first draft of the manuscript. All authors revised and approved the final manuscript.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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