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Spatial and ecological isolation in cicadas: First data from *Tibicina* (Hemiptera: Cicadoidea) in France

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Abstract. The seven taxa of the cicada genus *Tibicina* (*T. corsica corsica*, *T. corsica fairmairei*, *T. garricola*, *T. haematodes*, *T. nigronervosa*, *T. quadrisignata*, *T. tomentosa*) which occur in continental France and Corsica were investigated. Extrinsic factors (geographical barriers) and factors intrinsic to the ecology of species were considered in an effort to understand the biogeography of *Tibicina.* Three patterns related to intrinsic factors were recognised: (1) pairs of taxa with sympatric distributions but with divergent habitat preferences; (2) pairs of taxa with sympatric distributions and similar habitat but with allochronic occurrence; (3) pairs of taxa with similar ecology but with allopatric distributions. When taxa were separated by their habitat, the height of vegetation appeared to be more important than the floristic composition of the habitat. These factors lead to the partitioning of resources in time and space. All taxa occur in secondary vegetations. Human agro-pastoral activity has probably influenced the dynamics of cicada populations and the maintenance of isolation between them.

INTRODUCTION

The genetic integrity of species is commonly supposed to be maintained through premating and postmating isolating mechanisms (Dobzhansky, 1947; Mayr, 1942, 1963), the former corresponding broadly to Paterson's specific-mate recognition systems (SMRSs) (Paterson, 1985). In hemipteran insects, as with many other animals, the premating processes that maintain isolation between species are mainly investigated by studying traits such as their spatial distribution (De Boer, 1995), ecological preferences (Denno et al., 2001), exchanges of specific information in courtship (Claridge, 1990) and structural genitalic morphology (Soulier-Perkins & Bourgoin, 1998). Among hemipterans, behavioural premating isolating mechanisms in cicadas have been widely studied through the analysis of sound communication between the sexes during pair formation (Sueur, 2001). In contrast, spatial and ecological isolation has been less studied (Dybas & Lloyd, 1962; Callaham et al., 2000), particularly for cicadas inhabiting the West Mediterranean region (Claridge et al., 1979).

In spite of a significant recent contribution to the knowledge of French cicadas (see Boulard & Mondon, 1996), little is still known about the distribution and ecology of the Palaearctic genus *Tibicina.* Some data scattered in the literature are available for one species (*T. haematodes*) only (Vogel, 1935; Wagner, 1939; Batiashvili & Dekanoidze, 1967; Zhigaltzeva & Tereshko, 1962; Schedl, 1973, 1986). The genus *Tibicina* occurs from North Africa to Northern India (Boulard, 1976). The genus is widespread in France including the island of Corsica, with six species and one subspecies.

This paper aims to answer the question of whether the premating isolation of *Tibicina* species and sub-species is maintained through spatial and/or ecological processes. To document this, we gathered data on the distribution, abundance, habitat preferences and seasonality of *Tibicina* sub-species and species occurring in France. The results allowed us to investigate both the environmental parameters which hamper interspecific mating pair formation and the importance of human activities that play a role in the maintenance of ecological isolation between species.

MATERIALS AND METHODS

Taxa studied and distribution

According to Boulard & Mondon (1996) and Boulard (2000), the following *Tibicina* species and sub-species occur in France: *T. corsica corsica* (Rambur), *T. corsica fairmairei* Boulard, *T. garricola* Boulard, *T. haematodes* (Scopoli), *T. nigronervosa* Fieber, *T. quadrisignata* (Hagen) and *T. tomentosa* (Olivier).

Specimens of the various *Tibicina* taxa were collected in the south of continental France (summers 1996–2001) and in Corsica (June 2000). Identifications were made by comparison with identified specimens in the entomological collections of the Muséum national d'Histoire naturelle (MNHN). The *Tibicina* material of MNHN was examined via 30 specimens of *T. c. corsica*, 41 of *T. c. fairmairei*, 68 of *T. garricola*, 414 of *T. haematodes*, 48 of *T. nigronervosa*, 36 of *T. quadrisignata* and 21 of *T. tomentosa*. Distributions of species were superimposed upon the vegetation map of France (Defaut, 1996, 2001). The populations of *T. c. corsica* and *T. nigronervosa* have been previously

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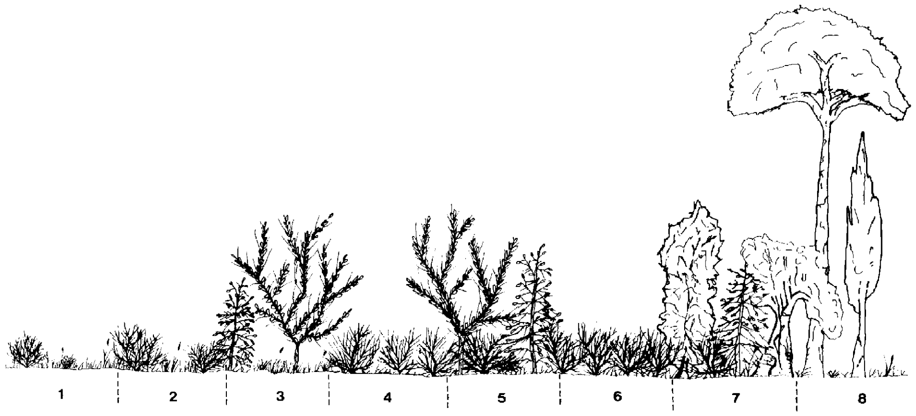

Fig. 1. Schematic representation of the eight habitat classes. See Table 1 for the definition of the vegetation classes.

mapped by Puissant & Sueur (2001). In addition, the relative frequency of each species was estimated following Voisin (1995). The ratio $f = n/N$ was calculated, where f is the probability of finding at least one specimen of one species when searching at random in a limited area during its adult phase, n is the number of sites where the species has been found and N is the total number of sites investigated in the area where a *Tibicina* species has been found. Because more than one species can occur at any given site, the sum of the relative frequencies is not 1.

Definition of habitats

Preliminary observations, together with some already published data (Wagner, 1939; Vogel, 1938; Schedl, 1986; Pillet, 1993), clearly showed that *Tibicina* species do not have strict preferences in the choice of their host plants. For this reason, a classification based upon the physical structure of vegetation (height of the vegetative structures and the percentage of ligneous plants) rather than upon floristic composition has been used to define the habitat of cicadas. Eight classes have been selected (Puissant & Sueur, 2001; Table 1 and Fig. 1), which correspond to the physiognomic types of Mediterranean shrub systems as defined by Tomaselli (1981). Habitat classes differ from vegetation classes in that they do not take into account either climatic features or floristical composition.

More than one habitat can occur in one site. The probability of occupancy of each habitat by a species was estimated with the ratio: $r = h/H$, where r is the probability of finding at least one specimen of one species in one habitat class when searching at random in a limited area, h is the number of contacts with the species in one habitat category and H is the total number of contacts with the species in all the habitat classes.

Table 1. Definition of the eight habitat used based upon the height of vegetation and the percentage of ligneous plants.

Habitat classes	Height (m)	% of ligneous plants
1 grassland	< 0.5	< 20
2 short moor	< 0.5	20–40
3 high moor	0.5–2	20–40
4 open short shrubland	< 0.5	40–60
5 open high shrubland	0.5–2	40–60
6 closed short shrubland	< 0.5	> 60
7 closed high shrubland	0.5–2	> 60
8 woodland	> 2	> 40

Seasonality

The seasonal occurrence of species was determined by field observations and by gathering the dates of capture of the specimens in the collections of the MNHN. The data for all years have been pooled together and presented with a 2–day precision.

RESULTS

Distribution

The geographical distributions of the species are shown in Figs 2–4, except for *T. c. corsica* and *T. nigronervosa* which were only found in Corsica and were thus separated by the Mediterranean Sea from the taxa occuring on the French mainland (i. e. *T. c. fairmairei*, *T. garricola*, *T. haematodes*, *T. quadrisignata*, *T. tomentosa*). In continental France, *T. haematodes* and *T. quadrisignata* showed allopatric and interleaved distributions with respect to each other. A disjunction related to the Rhône Valley is observed in the distributions of *T. garricola*, *T. haematodes* and *T. quadrisignata*. One population of *T. c. fairmairei* and one of *T. tomentosa* were found to be syntopic.

Vegetation classes used by each species are summarised in Table 2. *T. garricola*, *T. tomentosa* in continental France, and *T. c. corsica* and *T. nigronervosa* in Corsica proved to be typical Mediterranean species whose distributions were limited to the sub-humid temperate vegeta-

Table 2. Vegetation classes occupied by *Tibicina* taxa in France (mainland and Corsica). SH3: Xeric sub-humid temperate class, warm sub-class; SX3: Sub-xeric class, temperate sub-class; SX4: Sub-xeric class, cool sub-class; SX5: Sub-xeric class, cold sub-class; Cb: Colinus class.

	Vegetation classes				
	Xeric	Sub-xeric			Colinus
Taxa	SH3	SX3	SX4	SX5	Cb
T. c. corsica	■				
T. c. fairmairei	■	■			
T. garricola	■				
T. haematodes	■	■			■
T. quadrisignata	■	■	■	■	
T. nigronervosa	■				
T. tomentosa	■				

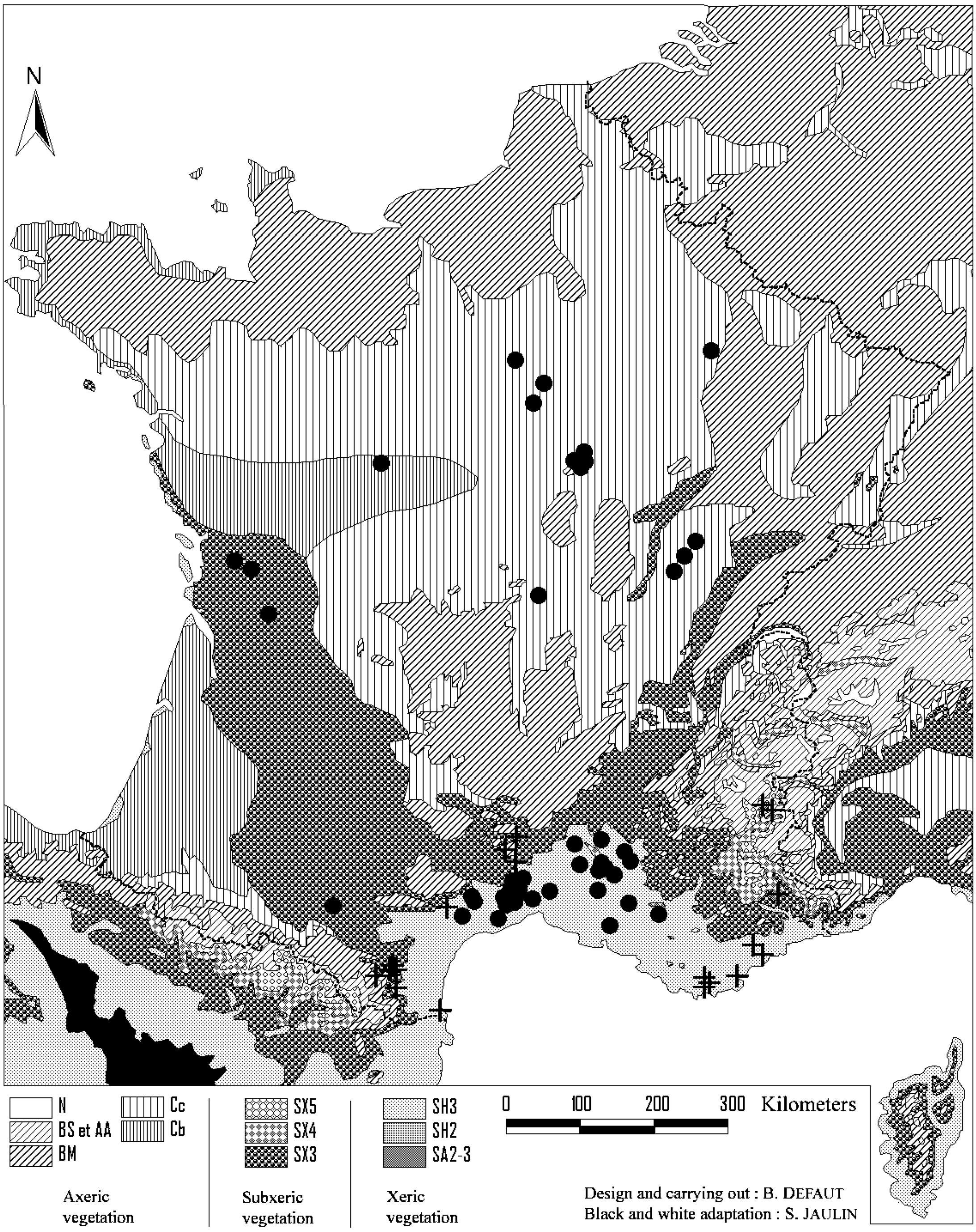

Fig. 2. Distribution of *T. haematodes* (dots) and *T. quadrisignata* (crosses) in France. Each dot or cross corresponds to a population. Areas correspond to vegetation classes. N: Nival class; BS and AA: Boreal-subalpine and artic-alpine classes; BM: Boreal montane class; Cc and Cb: Collinus classes; SX5: Sub-xeric class, cold sub-class; SX4: Sub-xeric class, cool sub-class; SX3: Sub-xeric class, temperate sub-class; SH3: Xeric sub-humid temperate class, warm sub-class; SH2: Xeric sub-humid temperate class, temperate sub-class; SA2-3: Sub-arid class, warm-temperate sub-class.

tion class (SH3). In contrast, *T. c. fairmairei*, *T. haematodes* and *T. quadrisignata* were found in two or more vegetation classes and their distribution appeared to be extensive.

Species frequencies are presented in Table 3. In continental France, *T. haematodes*, *T. garricola* and *T. quadrisignata* were the most frequent species while *T. tomentosa* and *T. c. fairmairei* were rare. In Corsica, *T. c. corsica* was more abundant than *T. nigronervosa*.

Habitat preferences

Habitats used by each species are summarised in Fig. 5. Differences in habitat selectivity were recognised for sympatric species: (1) for *T. garricola* (mainly habitat 7) and *T. haematodes* (mainly habitat 8), (2) for *T. c. fairmairei* (habitats 1, 3, 5) and *T. garricola* (mainly habitat

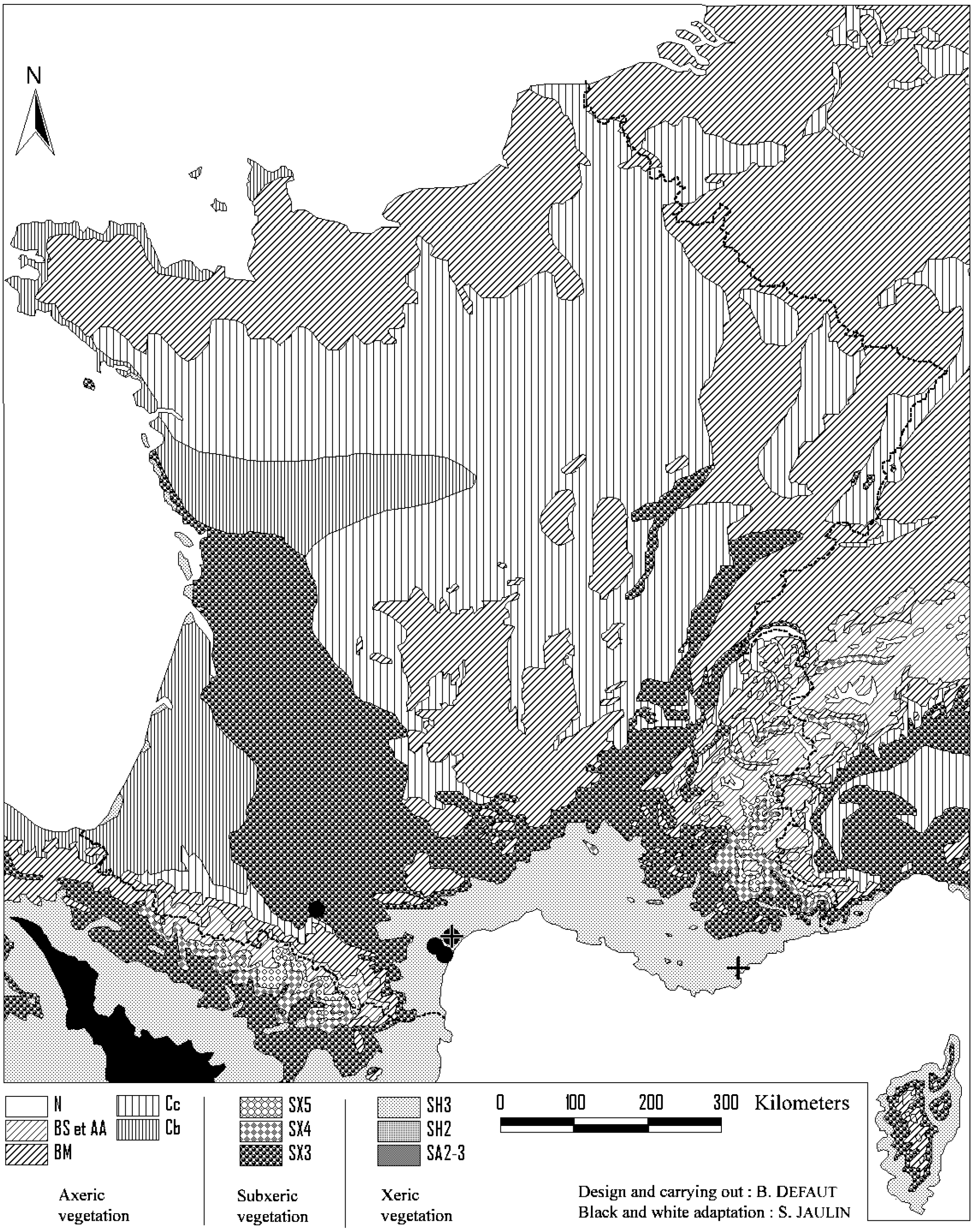

Fig. 3. Distribution of *T. corsica fairmairei* (dots) and *T. tomentosa* (crosses) in France. Vegetation classes as in Fig. 2.

TABLE 3. Frequencies of *Tibicina* taxa in France (mainland and Corsica).

Taxa	Mainland	Corsica	Cumulative data
T. c. corsica	0	0.647	0.175
T. c. fairmairei	0.065	0	0.048
T. garricola	0.283	0	0.191
T. haematodes	0.457	0	0.333
T. nigronervosa	0	0.353	0.095
T. quadrisignata	0.261	0	0.191
T. tomentosa	0.033	0	0.024

7), *T. haematodes* (mainly habitat 8), *T. quadrisignata* (mainly habitats 7, 8), (3) for *T. tomentosa* (habitats 1, 2, 3) and *T. garricola* (mainly habitat 7), *T. haematodes* (mainly habitat 8), *T. quadrisignata* (mainly habitat 7 and 8), (4) for *T. c. corsica* (habitat 1) and *T. nigronervosa* (habitats 5, 7).

In addition, *T. haematodes* in continental France and *T. nigronervosa*, *T. c. corsica* in Corsica are stenoecious species as they were only found in one or two habitat categories. In contrast, *T. c. fairmairei*, *T. garricola*, *T. quadrisignata* and *T. tomentosa* are euryoecious species

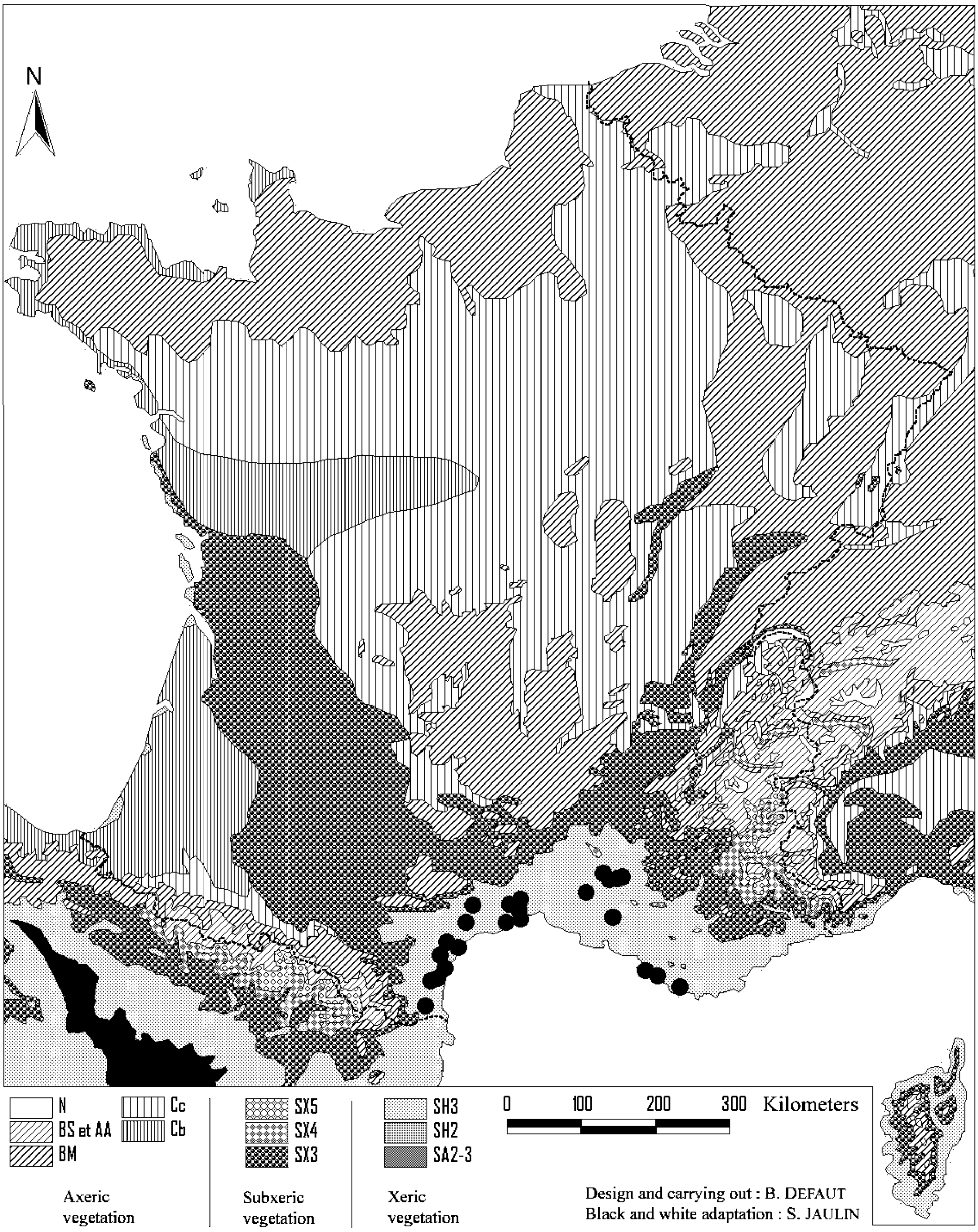

Fig. 4. Distribution of *T. garricola* in France. Vegetation classes as in Fig. 2.

as they are associated with more than two habitat categories. *T. c. fairmairei*, *T. garricola* and *T. tomentosa* were thus limited to only one or two vegetation classes but were found in more than two habitats. This is related to the fact that one vegetation class may include several habitat classes.

Seasonality

The adult seasonal pattern of species is given in Table 4. *T. haematodes* exhibited the longest period of adult activity while *T. tomentosa* and *T. quadrisignata* showed the shortest. Our results clearly indicate that *T. c. fairmairei* populations emerge later in the year than *T. tomentosa* populations. This time shift in seasonality leads to an allochrony between *T. c. fairmairei* and *T. tomentosa* in the site where the two species occur together. *T. c. corsica* emerged before *T. c. fairmairei.* Similarly, *T. garricola* emerged earlier than *T. quadrisignata*, a time shift particularly pronounced in the Eastern Pyrenees. The sympatric but not syntopic Corsican species *T. c. corsica* and *T. nigronervosa* showed almost the same seasonal rhythm.

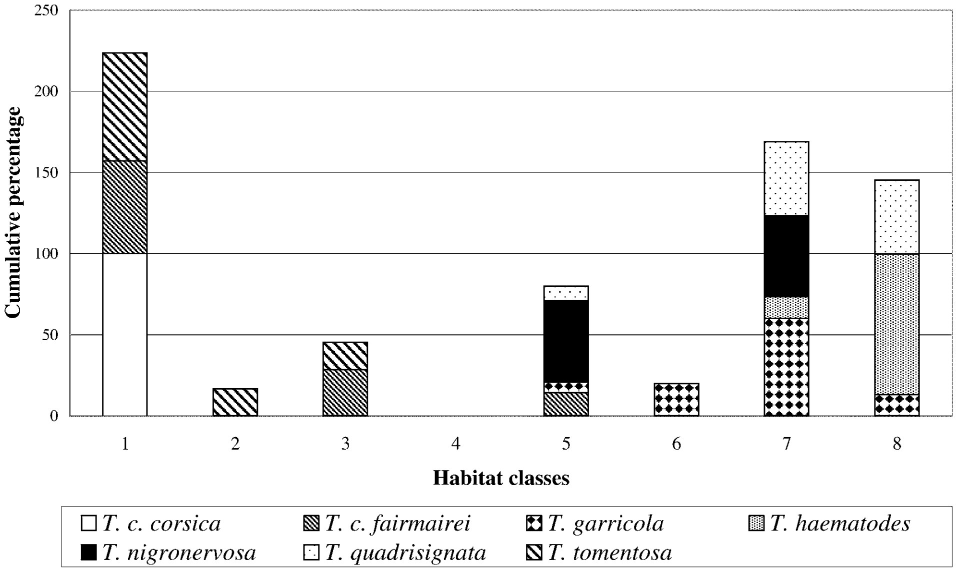

Fig. 5. Habitats used by *Tibicina* taxa in France (mainland and Corsica). See Table 1 and Fig. 1 for the definition and representation of habitat classes.

As shown in Table 5, taxa were therefore isolated by extrinsic factors (geographical barriers) or intrinsic factors. Three modalities of intrinsic factors were recognised: (1) taxa with sympatric distributions but with divergences in their habitat preferences (allotopy); (2) taxa with sympatric distributions and similar habitat but with a shift in their emergence pattern (allochrony); (3) taxa ecologically similar but with non-overlapping distributions (allopatry).

DISCUSSION

Spatial, habitat and temporal isolation

Each of the developmental stages in cicadas (eggs, larva, adults) use vascular plants as a food resource or habitat (Myers, 1929): (1) embryonic development is achieved inside the plant (endophytous phase); (2) larval development occurs underground where larvae feed on root (endogenous phase); and (3) winged adults live for approximately two or three weeks during which they feed on the sap of vascular plants (aerial phase). Surprisingly, cicadas did not develop a strong host plant specificity. Although some host preferences have been reported (Myers, 1929; Dybas & Lloyd, 1974; Lloyd & White, 1976; Moulds, 1990; Boulard & Mondon, 1996; Cook et al., 2001), strict monophagy and strong host choice by females for oviposition is not generalized in cicadas. Our observations clearly showed that the species of *Tibicina* use most of the available plant species for feeding, calling and ovipositing. In spite of this absence of narrow host relationships, our results show that taxa are clearly isolated through spatial and ecological processes. First, the taxa can be isolated by geographical barriers, which are extrinsic factors. This is the case of Corsican taxa and mainland taxa. Second, species can be isolated by intrinsic factors, with three primary patterns: (1) the taxa showed sympatric distributions with divergences in their habitat preferences (e. g. *T. garricola* and *T. haematodes* or *T. c. corsica* and *T. nigronervosa*); (2) the taxa were sympatric with similar habitat selection but were allochronic (*T. garricola* and *T. quadrisignata*; *T. c. fairmairei* and *T. tomentosa*); (3) the species presented similar ecological traits but showed allopatric distributions (*T. haematodes* and *T. quadrisignata*).

When taxa were separated by habitat preferences, the structure of the habitats (in particular the height of vegetation) appeared to be more important than the floristic composition. Such isolation through habitat preferences has been observed in North American species (Dybas & Lloyd, 1962, 1974; Lloyd & White, 1976; Callaham et al., 2000). The calling song produced by males was suggested as a potential mechanism acting against dispersal (Myers, 1929) which is particularly low in cicadas (Karban, 1981; Lloyd et al., 1982; Taylor, 1985). Furthermore, *Tibicina* calls clearly have a role in

TABLE 4. Seasonality of *Tibicina* taxa in France (mainland and Corsica). Data from examination of MNHN collections and personal observations. Limits correspond to the range of dates of collection or observation of more than two males.

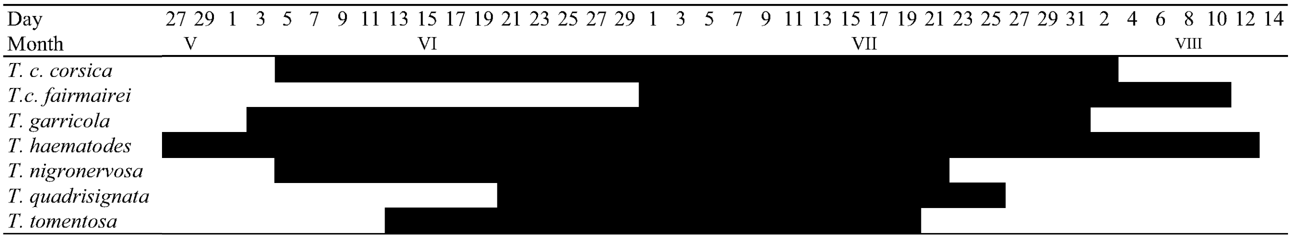

Table 5. Spatial and ecological isolation parameters for the *Tibicina* taxa occuring in France.

	T. c. corsica	*T. c. fairmairei*	*T. garricola*	*T. haematodes*	*T. nigronervosa*	*T. quadrisignata*	*T. tomentosa*
T. c. corsica	–						
T. c. fairmairei	geographical barrier	–					
T. garricola	geographical barrier	allotopy	–				
T. haematodes	geographical barrier	allotopy	allotopy	–			
T. nigronervosa	allotopy	geographical barrier	geographical barrier	geographical barrier	–		
T. quadrisignata	geographical barrier	allotopy	allochrony	allopatry	geographical barrier	–	
T. tomentosa	geographical barrier	allochrony	allotopy	allotopy	geographical barrier	allotopy	–

attracting and maintaining males at chorus centres. If the origin of habitat separation is still unkown, choruses could participate in maintaining the *Tibicina* species in distinct habitats.

When taxa are not isolated by their habitat characteristics, a shift in their emergence patterns is observed (allochrony). An example is given by the syntopic populations of *T. c. fairmairei* and *T. tomentosa*, the former clearly emerging after the latter. Seasonal data on *T. c. fairmairei* and *T. tomentosa* allopatric populations are unfortunately missing. Nevertheless, the emergence time pattern of *T. c. fairmairei* appears to be delayed in comparison to that of *T. c. corsica*. This might indicate that the seasonal activity of *T. c. fairmairei* directly depends on the presence of *T. tomentosa*. This suggests that in each species the time of juvenile development is firmly fixed.

Finally, *T. haematodes* and *T. quadrisignata* show non-overlapping distributions. Further studies are needed to explain this allopatry between two species that occur in similar habitats, are widely distributed along several vegetation classes, and are active throughout all summer. The isolation allows species not to compete at the same time and at the same place during their peak of emergence. This leads to a partitioning of feeding, calling and ovipositing resources. In particular, it avoids potential acoustic interference between the calling songs produced by the males of different species, as their acoustic signals exhibit roughly similar time and frequency structure (Boulard, 1995).

Habitat isolation and human activities

In France, all *Tibicina* species are distributed in secondary vegetation formations. Thus, their distributions and their relative frequencies are closely related to human pressure on landscape structure. Open and semi-open Mediterranean habitats essentially result from an ecological succession related to fire-setting (Trabaud, 1981) or the abandonment of cultivation (Escarré et al., 1983). Shrublands occurred throughout the last two million years in the Mediterranean Basin, but human land practices have recently considerably increased (Castri, 1981). This evolution benefited *T. garricola* and *T. nigronervosa* which predominantly live in shrublands at high densities. In contrast, *T. tomentosa* and *T. c. fairmairei* showed the lowest frequencies and presently are represented only by relict and endangered populations. These species were probably previously more abundant, at the end of the 19th century (Boulard & Mondon, 1996). They are adapted to open habitats such as fallow, grazed or temporarily abandoned fields. In southern France, a decline in cultivation and an expansion of vineyards probably dramatically decreased the size of their populations. In Corsica, where browsing and grazing by herds of domestic livestock still occurs, many open fields are still available and *T. c. corsica* remains abundant. A decline of pastoral activity in Corsica would lead *T. c. corsica* to decline or to invade the habitat already occupied by *T. nigronervosa*. Lastly, *Tibicina haematodes* and *T. quadrisignata* are mainly found in woodlands. These euryecious species are observed along several vegetation classes and are not limited in their geographical extension to the Mediterranean region. A similar link between forest habitat and wide distribution has been already reported for birds (Blondel & Aronson, 1999).

To conclude, and as already reported for North American species (Callaham et al., 2000), the distribution and isolation of *Tibicina* species are linked to a complex association between abiotic and biotic factors, including human pressures.

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