# ORIGINAL PAPER

# The pygmy mole cricket *Xya variegata* as an indicator for dynamic river systems

Thorsten Münsch · Thomas Fartmann · Björn Machalett · Dominik Poniatowski

Received: 13 March 2012/Accepted: 10 October 2012/Published online: 23 October 2012 © Springer Science+Business Media Dordrecht 2012

**Abstract** There is an urgent need to conserve and restore dynamic floodplains as one of the last wildernesses in Europe and to maintain their unique plant and animal communities. Disturbance-dependent ecosystems such as natural floodplains harbour many highly specialised and endangered insect species. One of these species is the pygmy mole cricket Xya variegata Latreille, 1809 (Orthoptera: Tridactylidae), a floodplain specialist of the Ponto-Mediterranean region. However, as with many endangered insect species detailed knowledge on the requirements of X. variegata is largely unknown, even though such knowledge is of particular importance for successful nature conservation. The aim of this study was to analyze the ecological requirements of X. variegata and to verify the species' suitability as an indicator for dynamic river systems of the Ponto-Mediterranean region. Therefore, microhabitat analyses were conducted in August 2010 on 42 plots in a nearly natural floodplain of the western Spanish Pyrenees. The results show that patch occupancy in X. variegata was determined by a high amount of fine sediment particles and low vegetation coverage. Moreover, population sizes were positively correlated with low vegetation and gravel/stone coverage. The plots with the highest population sizes (29 and 36 individuals/0.5  $\text{m}^2$ ) had no vegetation at all. Habitats of *X. variegata* were usually located distant to the main channel; that is areas where fine sediment particles are deposited after a flood event. Disturbance is thus mandatory for the persistence of the species and makes *X. variegata* a suitable indicator for dynamic river systems.

**Keywords** Braided river · Disturbance · Hydrological dynamic · Natural habitat · Succession · Unregulated floodplain

# Introduction

Europe is one of the most densely populated places on earth (Klein Goldewijk 2005). Consequently, cultivated landscapes dominate, while semi-natural and natural habitats are rather rare (EEA 2012). Examples of near natural habitats with low human impacts include unregulated floodplains characterized by high hydrological dynamics and geomorphological processes (Hughes and Rood 2001; Tockner et al. 2008). Typical for these disturbance-dominated ecosystems is the coexistence of different aquatic and terrestrial habitat types within a mosaic of different successional stages as a result of periodic floods (Hughes 1997; Ward et al. 1999, 2002). However, natural floodplains are not only characterized by a high level of disturbance and spatio-temporal heterogeneity, but also by a complex thermal mosaic with maximum temperatures above 40 °C (Tonolla et al. 2010). These diverse conditions allow the occurrence of many highly specialized arthropods (e.g. Reich 1991: Saltatoria; Lude et al. 1999: Formicidae; Nickel 1999: Auchenorrhyncha; Manderbach and Framenau 2001: Araneae; Sadler et al. 2004: Coleoptera). Dynamic floodplains are therefore considered as

T. Münsch · T. Fartmann · D. Poniatowski (☒)
Department of Community Ecology, Institute of Landscape
Ecology, University of Münster, Robert-Koch-Straße 28,
48149 Münster, Germany
e-mail: poni@uni-muenster.de

# B. Machalett

Department of Climatology, Institute of Geography, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany

# B. Machalett

Department of Natural and Applied Sciences, Bentley University, 175 Forest Street, Waltham, MA 02452-4713, USA



regional biodiversity hotspots (Ward et al. 1999; Robinson et al. 2002; Tockner and Stanford 2002).

However, during the last two centuries the European floodplains lost most of their former extension (Wenger et al. 1990; Klimo and Hager 2001), with losses of up to 95 % (Tockner and Stanford 2002). From an ecological point of view many of the remaining European floodplains are functionally extinct (Tockner et al. 2008); meaning that periodic floods which are interlinked with geomorphological processes are missing. The main reason for this development is human intervention in floodplain dynamics (Nilsson and Berggren 2000; Malmqvist and Rundle 2002; Paetzold et al. 2008). In the floodplains of alpine rivers for example, 95 % of the loss of gravel banks was caused by river regulation, channelization and impoundment (Kuhn 2005). Meanwhile, less than 10 % of the total length of alpine rivers is in semi-natural or natural conditions (Martinet and Dubost 1992). Due to the decrease of their natural habitats, the floodplain specialists are among the most endangered animal species in Europe (Reich 1991; Lude et al. 1999; Manderbach and Framenau 2001; Carron et al. 2001; Eyre et al. 2001; Sadler et al. 2004).

The pygmy mole cricket *Xya variegata* Latreille, 1809 (Orthopera: Tridactylidae) is one of these specialists. As a pioneer species of sparsely vegetated muddy banks its occurrence is restricted to riverine floodplains (Szijj 1992; Poniatowski et al. 2009) and a few secondary habitats such as sand pits with small water pools and newly-created ponds (Berg et al. 2000; Russ 2006; Zechner 2009). However, as with many endangered insect species (cf. Gröning et al. 2007) detailed knowledge on the requirements of *X. variegata* is widely unknown, even though such knowledge is of particular importance for successful nature conservation (Samways 2005; Hein et al. 2007).

The aim of this study was to analyze the ecological requirements of the floodplain specialist *X. variegata* to derive conservation measures that ensure the persistence of the species. Specifically, our study tries to address the following questions: (1) How are the microhabitats of *X. variegata* characterized in relation to habitat structure, soil texture and moisture? (2) Can *X. variegata* be considered as an indicator for dynamic river systems? (3) What conservation measures are necessary to promote *X. variegata*?

# Materials and methods

# Study organism

The pygmy mole cricket *Xya variegata* Latreille, 1809 (Orthoptera: Tridactylidae) is a small-sized insect species (Fig. 1a) with a Ponto-Mediterranean distribution (Thorens

and Nadig 1997; Baur et al. 2006). Adults are 4–6.5 mm in total length (Harz 1975) and occur perennially (Blackith and Blackith 1979; Thorens and Nadig 1997). The species has sturdy, well-developed hind legs and mole-like front legs (Fig. 1b). Because of the well-developed hind legs the species has good jumping power. *X. variegata* uses its mole-like front legs to graze the algae surface of sediment particles and to build burrow systems (hereafter called galleries, Fig. 1a) (Messner 1963; Blackith and Blackith 1979).

# Study area

The study area is located in the western Spanish Pyrenees, about 10 km west of Jaca (province Huesca). It comprises the 12 km long lower part of the floodplain of the southwards directed *Valle de Aisa*, through which the *Rio Estarrún* runs (42°40′00 N/0°37′26 W: 960 m a.s.l. and 42°34′01 N/0°39′58 W: 695 m a.s.l.). Within the study area the *Rio Estarrún* is interrupted by a weir (42°37′20 N/0°39′25 W: 830 m a.s.l.). Further regulatory measures are missing. Despite the weir, the study area is highly hydrologically dynamic, resulting in a mosaic of different substrates and successional stages. The floodplain can thus be described as semi-natural or as nearly natural. The river bed of the *Rio Estarrún* consists of limestone and calcareous marl (García-Ruiz and Lasanta-Martínez 1990).

The study area is in the transition zone between sub-Cantabrian and sub-Mediterranean climate, with an average annual precipitation of 835 mm and a mean annual temperature of 9.8 °C. The summer months between June and September are dry and hardly influenced by rain. In summer, hot periods with temperatures reaching almost 40 °C can occur and especially poorly vegetated gravel and sand banks of the floodplain tend to heat up significantly during these months. In winter and spring time the precipitation increases up to 100 mm per month. Intense rainfalls are characteristic for the periods October to December and April to May (Climate station Jaca-Ordolés, 1,040 m a.s.l.; Villar et al. 1997).

The vegetation of the floodplain is dominated by mosaics of willow shrubs (*Salicion albae*), barberry shrubs (*Berberidion vulgaris*) and sub-Mediterranean dry grasslands (*Aphyllanthion*). Calcareous fens with *Lythrum salicaria*, *Molinia caerulea* and *Scirpoides holoschoenus* occur primarily in the marginal regions of the floodplain (Villar et al. 1997, 2001).

#### Sampling design

The study was conducted at the end of August 2010 in a 12 km long part of the *Rio Estarrún*. To record all



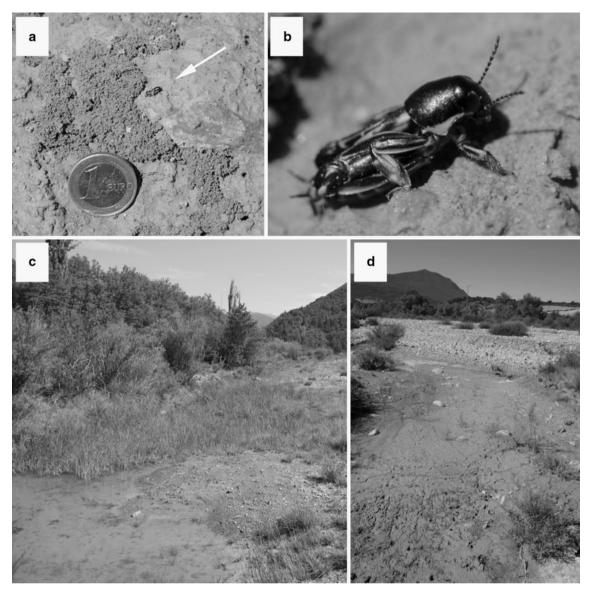


Fig. 1 a Xya variegata beside its galleries (Arrow); b X. variegata in total view; c Calcareous fen in the floodplain of the Río Estarrún, the sparsely vegetated site in front was colonised by X. variegata; d Mud bank in the study area with optimal habitat conditions for X. variegata

populations of X. variegata we walked downstream through the whole floodplain, starting below the village Aísa. Since X. variegata colonizes sparsely vegetated habitats (Szijj 1992; Berg et al. 2000; Poniatowski et al. 2009; Zechner 2009), all sites with bare soil were searched visually. Searching for the galleries was a convenient way to detect the species. In total, we found 29 populations of the species. Absence plots of X. variegata (n = 13) were chosen randomly throughout the whole study area but it was ensured that the plots represented potential habitats of the species (i.e., more or less sparsely vegetated mud banks). The absence plots were sampled in the same way as sites with the occurrence of X. variegata (see below). The sampling took place between 9:00 and 17:00 h (CET + 1). The weather conditions were favourable (hot, sunny and

calm days without rain) and matched the species preferences for activity. Each plot was sampled once.

# Orthoptera sampling

In the study area X. variegata usually lives in very small colonies that rarely exceed an area of  $0.5 \text{ m}^2$ . We therefore used a  $0.5 \text{ m}^2$  box quadrat  $(0.71 \times 0.71 \text{ m})$  with white gauze covered sides of 0.8 m height (Poniatowski and Fartmann 2010) to assess the population size of the species. The box quadrat was placed once per colony, in the centre of the species galleries. Before we started with catching X. variegata individuals, the coverage of the galleries was ascertained as a control factor. Since the gallery cover was highly correlated with the population size (Pearson's



correlation, r = 0.83, n = 29, P < 0.001), we only used the variable population size for the analysis. In the majority of the cases the animals hopped on the gauze and were caught from the sides. However, it was necessary to demolish the galleries with a grass stalk because some individuals were hidden in them. For each plot (including the absence plots) all (other) orthopteran species within the box quadrat were recorded qualitatively. The attendant species were determined using Poniatowski et al. (2009).

# Environmental parameters

The recording of environmental parameters took place within the box quadrat after the Orthoptera sampling. For each plot several environmental parameters that determine habitat selection in orthopterans (Gardiner et al. 2002; Poniatowski and Fartmann 2008; Fartmann et al. 2012), such as vegetation coverage, density, soil texture and moisture, were measured (Table 1).

Particle size distributions of surface soil samples were measured using a high resolution Beckman Coulter LS 13320 laser diffraction particle size analyser following the method described in Machalett et al. (2008). All samples were presieved with a 1.5 mm mesh in order to remove plant and root remnants and repeatedly treated with  $\rm H_2O_2(3~\%)$  to eliminate fine dispersed organic matter within the sediment. Following a thorough sample dispersion, an auto-prep station was used to measure each sample under identical conditions.

Table 1 Overview of parameters examined for statistical analyses

Data analysis

Differences between more than two variables were analysed using Kruskal–Wallis *H*-test. Dunn's test was used as a post hoc test.

To evaluate which environmental factors affect the occurrence and the abundances of X. variegata, two generalised linear models (GLMs) were conducted. The first model had a binomial error structure to compare the occupied (presence) and unoccupied (absence) plots. The second model considered only the occupied plots to analyse the effects of several environmental variables on population sizes. For the second model a quasi-Poisson error structure was used to counteract over-dispersion (Zuur et al. 2009). To avoid problems associated with multicollinearity, a principal component analysis (PCA) was conducted to amalgamate highly correlated variables such as 'total vegetation coverage', 'vegetation density' and 'bare soil' into one factor (cf. Stefanescu et al. 2004; Poniatowski and Fartmann 2011). The newly created factor (hereafter called 'vegetation structure') represents a clear gradient from sparsely (negative values) to densely vegetated sites (positive values) (Table 1). The same is true for the grain size fractions. Sand, silt and clay were combined to one factor (Table 1). The new factor (hereafter called 'soil texture') represents a clear gradient from sites with high amounts of coarse particles (sand-rich, negative

Parameter	r	Newly created factor
Response variable model 1 (binomial GLM)		
Presence versus absence		
Response variable model 2 (quasi-Poisson GLM)		
Population size (individuals/0.5 m <sup>2</sup> )		
Predictor variables (model 1 and model 2)		
Total vegetation (%)	0.925	Vegetation structure
Vegetation density (%) <sup>a</sup>	0.760	
Bare soil (%)	-0.873	
Gravel/stones (%)	,	
Sand (%) <sup>b</sup>	-0.998	Soil texture
Silt (%) <sup>b</sup>	0.996	
Clay (%) <sup>b</sup>	0.988	
Soil moisture <sup>c</sup>	)	

To avoid problems in generalized linear models (GLMs) with multicollinearity several environmental variables were summarised by using principal component analysis (PCA) (for details see text). Pearson's correlation coefficients (r) between the sampled variables and their substitutes are given

<sup>&</sup>lt;sup>c</sup> Sampled in situ: Six-part classification according to Ad-hoc-AG Boden (2005); in brackets the potential free energy of water is given (log hPa): 'very wet' (0), 'wet' (≤1.4), 'very moist' (2.1 to >1.4), 'moist' (2.7 to >2.1), 'slightly moist' (4.0 to >2.7) and 'dry' (>4.0)



<sup>&</sup>lt;sup>a</sup> Measured within a frame of 30 cm depth and 50 cm width for layers in 0–5, 5–10, ..., 25–30 cm height above ground (Poniatowski and Fartmann 2008), the sum of all layers was used in GLM (Poniatowski and Fartmann 2010)

<sup>&</sup>lt;sup>b</sup> Measured in the laboratory with a high resolution Beckman Coulter LS 13320 laser diffraction particle size analyser. For a detailed description of the method see text

values) to sites with high amounts of fine particles (silt and clay-rich, positive values) (Table 1).

All analyses were performed using R-2.12.1 (R Development Core Team 2010), SPSS 16.0 and SigmaPlot 11.0 statistical packages.

#### Results

#### Distribution

With 29 populations, *Xya variegata* was widespread in the study area. Colonies of the species were found along an altitudinal range from 910 m a.s.l. near the village Esposa (42°39′21 N/0°38′02 W) up to the vicinity of the outfall of the *Rio Estarrún* into the *Rio Aragón* in 700 m a.s.l. (42°34′18′N/0°39′52 W); i.e. the populations followed the course of the river on a length of about 10 km.

#### Habitat requirements

#### Presence versus absence

The GLM analyses revealed that the occurrence of X. variegata was positively correlated with 'soil texture' and negatively correlated with 'vegetation structure' [Pseudo  $R^2$  (McFadden) = 0.37, Table 2]; i.e., patch occupancy in X. variegata was determined by a high amount of fine sediment particles (median clay and silt: 41 %) and low vegetation coverage (median total vegetation: 15 %). All other environmental parameters were excluded from the final model by stepwise backward-selection and were thus less important for patch occupancy in the investigated species.

# Population sizes

In total, we caught 285 individuals. Occupied plots had between 1 and 36 individuals/0.5 m<sup>2</sup>, but 90 % of the occupied plots had low population sizes with 1-16 individuals/0.5 m<sup>2</sup> (mean  $\pm$  SE: 9.3  $\pm$  1.5 individuals/0.5 m<sup>2</sup>). The GLM showed that the population sizes of *X. variegata* were negatively correlated with 'gravel/stones' and 'vegetation structure' (Pseudo  $R^2$  [McFadden] = 0.63, Table 3); i.e. sparsely vegetated sites with a low amount of gravel/ stones had higher population sizes than vegetation- and/or gravel-rich sites. The plots with the highest population sizes (29 and 36 individuals/0.5 m<sup>2</sup>) had no vegetation at all (Fig. 1d). In contrast, the effects of clay, silt and sand as well as soil moisture were less important and did not contribute to the final model. However, when predictor variables were analysed separately, soil moisture had an impact on abundances as well [GLM: P < 0.001; Pseudo  $R^2$ 

**Table 2** Statistics of GLM: Relationship between the occurrence of *Xya variegata* [binomial response variable: presence ( $N_{\text{plots}} = 29$ ) versus absence ( $N_{\text{plots}} = 13$ )] and several environmental parameters (predictor variables) Pseudo  $R^2$  (McFadden) = 0.37

Variable	Estimate	SE	Z	P
Vegetation structure	-2.2647	0.77	-2.946	< 0.001
Soil texture	1.3126	0.56	2.328	< 0.01

Non-significant predictors were excluded from the final model by stepwise backward-selection (P>0.05): gravel/stones and soil moisture

(McFadden) = 0.55]. Abundances of *X. variegata* were high when soil moisture was at a moderate level (Fig. 2).

# Attendant species

The most common attendant species in habitats of *X. variegata* were *Tetrix ceperoi*, *T. undulata* and *Pteronemobius lineolatus* with a constancy of 10–21 % (Table 4). Typical species for the absence plots were *Gryllotalpa gryllotalpa* and *Chorthippus jucundus*, occurring in 39 and 30 % of the plots, respectively (Table 4).

#### **Discussion**

# Habitat selection in Xya variegata

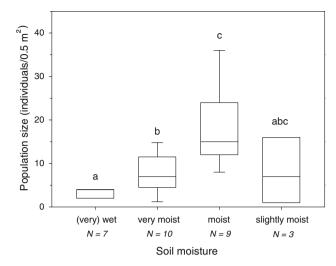
Of special importance for habitat selection in *X. variegata* seems to be a high amount of bare soil. This factor did not only explain the presence of the species, but also population size was correlated with it. This finding is supported by field observations from previous studies (e.g. Szijj 1992; Berg et al. 2000; Zechner 2009). On the one hand bare soil offers sufficient space to burrow and on the other hand *X. variegata* probably needs—as a thermophilous Ponto-Mediterranean species (Thorens and Nadig 1997; Baur et al. 2006)—a warm microclimate that is only provided by locations with a high proportion of bare soil, hence, sites

**Table 3** Statistics of GLM: relationship between the population size of *Xya variegata* (quasi-Poisson response variable;  $N_{\rm plots} = 29$ ) and several environmental parameters (predictor variables) Pseudo  $R^2$  (McFadden) = 0.63

Variable	Estimate	SE	Z	P
Vegetation structure	-0.727	0.15	-4.806	< 0.001
Gravel/stones	-0.033	0.01	-3.002	< 0.01

Non-significant predictors were excluded from the final model by stepwise backward-selection (P>0.05): soil texture and soil moisture





**Fig. 2** Relationship between soil moisture and population size of Xya variegata ( $N_{\text{plots}} = 29$ ). Box-plots show 10 and 90th percentile (whiskers), 25th and 75th percentile (boundary of the box) and median (line). Kruskal-Walli H-test:  $\chi^2 = 15.283$ , df = 3, P < 0.01. Different letters indicate significant differences at the P < 0.05 level (Dunn's test for significance,  $\alpha = 0.05$ ). Due to a small sample size the categories 'wet' and 'very wet' are combined

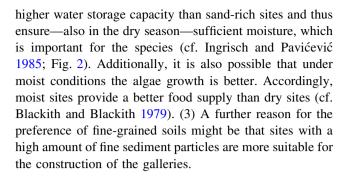
**Table 4** Frequency of Orthoptera species observed in plots occupied (N = 29) and unoccupied (N = 13) by *Xya variegata* 

	Presence $(N = 29)$		Absence $(N = 13)$	
	Absolute	%	Absolute	%
Tetrix ceperoi	6	21	1	8
Tetrix undulata	3	10	1	8
Pteronemobius lineolatus	3	10		
Eumodicogryllus bordigalensis	2	7		
Paratettix meridionalis	2	7		
Depressotetrix depressa	1	3		
Tetrix subulata	1	3		
Gryllotalpa gryllotalpa <sup>a</sup>	1	3	5	39
Chorthippus jucundus			3	30
Calliptamus barbarus			1	8
Oecanthus pellucens			1	8

<sup>&</sup>lt;sup>a</sup> Gryllotalpa gryllotalpa was only detected by its burrow system

that heat up more quickly than vegetated sites (Bryant and Shreeve 2002).

Moreover, habitat selection in *X. variegata* is determined by soil particle size, with a preference for sites with fine sediments. It is likely that several explanations are valid for this preference: (1) *X. variegata* mainly feeds on the algae growth of fine sediment particles ( $4 \times 4 \mu m$  to  $24 \times 48 \mu m$ ; Blackith and Blackith 1979), which are collected and grazed with its mouthparts (Messner 1963). (2) Soils with a high amount of fine sediment particles have a



### Indicator value of Xva variegata

In summary, it can be stated that X. variegata has high habitat specificity. But can X. variegata act as indicator for dynamic river systems in the Ponto-Mediterranean region? The species' habitats, bare soil-rich sites with a high amount of fine sediment particles, can only develop and be maintained as a result of periodic floods with substrate dynamics. Sites with such conditions are usually located distant to the main channel; that is areas where fine sediment particles are deposited after a flood event (Ward et al. 1998). This can be the riparian zone of slow-flowing lateral channels or small depressions within the floodplain. However, X. variegata is only able to colonize such sites in the initial stage of succession (Poniatowski et al. 2009; Fig. 1c, d). With ongoing succession competitive plants colonize the bare soil and X. variegata will be replaced by other Orthoptera species (e.g. Chorthippus jucundus, Table 4). Disturbance is thus mandatory for the persistence of the species in riverine floodplains.

# Implications for conservation

Xya variegata is—as an indicator for dynamic river systems—rather sensitive to floodplain regulation. The last populations in Switzerland for example, became extinct in the late 19th century due to river channelization (Thorens and Nadig 1997; Baur et al. 2006) and in Austria most of the few populations are restricted to secondary habitats (Berg et al. 2000; Russ 2006; Zechner 2009). In the Pyrenees the situation is a bit better. On the south side of this mountain range there are still some river systems with a semi-natural or partly natural character (pers. observ.) that harbor populations of X. variegata (Barranco Vega and Llucià-Pomares 2001: Rto Esera; S. Weigelmeier per. comm.: Rto Cinca; this study: Rto Estarrún; pers. observ.: Rto Lubierre). Taking this into account, the only way to preserve these populations is to maintain substrate dynamics.

It is obvious that a dynamic river system promotes not only *X. variegata*, but also a couple of other, partially high disturbance-dependent orthopteran species (Table 4). One of them is *Tetrix ceperoi*; an endangered ground hopper



species, which has similar habitat requirements as *X. variegata* (Gröning et al. 2007). But also Orthoptera that colonize different pioneer stages such as gravel banks or sparsely vegetated dry grasslands benefit from or depend on natural dynamics (Reich 1991; Stelter et al. 1997; Carron et al. 2001; Grosser and Rey 2009; Lemke et al. 2010). This is also true for specialists of other arthropod groups (Lude et al. 1999; Nickel 1999; Manderbach and Framenau 2001; Sadler et al. 2004). We therefore appeal to conserve and restore dynamic floodplains as one of the last wildernesses in Europe and to maintain their unique plant and animal communities.

**Acknowledgments** We are grateful to Gregor Stuhldreher (University of Münster) for logistical support. BM acknowledges funding of The Leverhulme Trust and the German Academic Exchange Service (DAAD).

#### References

- Ad-hoc-AG Boden (2005) Bodenkundliche Kartieranleitung, 5th edn. Hannover
- Barranco Vega P, Llucià-Pomares D (2001) Catálogo de los Caelifera no Acrididae (Insecta: Orthoptera) de Aragón. Cat Entomofauna aragonesa 23:15–18
- Baur B, Baur H, Roesti C, Roesti D (2006) Die Heuschrecken der Schweiz. Haupt, Bern
- Berg H-M, Gross H, Paill W (2000) Die Dreizehenschrecke *Xya variegata* Latreille, 1809 (Orthoptera: Tridactylidae), neu für Österreich. Beitr Entomofaun 1:3–8
- Blackith RE, Blackith RM (1979) Tridactyloids of the western old world. Acrida 8:189-217
- Bryant SR, Shreeve TG (2002) The use of artificial neural networks in ecological analysis: estimating microhabitat temperature. Eco Entomol 27:424–432
- Carron G, Sardet E, Praz C, Wermeille E (2001) *Epacromius tergestinus* (Charpentier, 1825) and other interesting Orthoptera in the floodplains of braided rivers of the Alps. Articulata 16: 27–40
- EEA (European Environment Agency) (2012) Corine land cover 2000 by country. http://www.eea.europa.eu. Accessed 3 February 2012
- Eyre MD, Lott DA, Luff ML (2001) The rove beetles (Coleoptera, Staphylinidae) of exposed riverine sediments in Scotland and northern England: habitat classification and conservation aspects. J Insect Conserv 5:173–186
- Fartmann T, Krämer B, Stelzner F, Poniatowski D (2012) Orthoptera as ecological indicators for succession in steppe grassland. Ecol Indicators 20:337–344
- García-Ruiz JM, Lasanta-Martínez T (1990) Land-use-changes of the Spanish Pyrenees. Mt Res Dev 10:241–255
- Gardiner T, Pye M, Field R, Hill J (2002) The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. J Orthoptera Res 11:207–213
- Gröning J, Krause S, Hochkirch A (2007) Habitat preferences of an endangered insect species, Cepero's ground-hopper (*Tetrix ceperoi*). Ecol Res 22:767–773
- Grosser N, Rey A (2009) Zur Fauna der Heuschrecken des Tagliamento und seiner Aue (Friaul/Italien). Articulata 24:69–78
- Harz K (1975) Die Orthopteren Europas II (Unterordnung Caelifera). Dr. W. Junk B.V, The Hague

- Hein S, Binzhöfer B, Poethke H-J, Biedermann R, Settele J, Schröder B (2007) The generality of habitat suitability models: a practical test with two insect groups. Basic Appl Ecol 8:310–320
- Hughes FMR (1997) Floodplain biogeomorphology. Prog Phys Geog 21:501–529
- Hughes FMR, Rood SB (2001) Floodplains. In: Warren A, French JR (eds) Habitat conservation: managing the physical environment. Wiley, Chichester, pp 105–121
- Ingrisch S, Pavićević D (1985) Zur Faunistik, Systematik und ökologischen Valenz der Orthopteren von Nordost-Griechenland. Mitt Münch Ent Ges 75:45–77
- Klein Goldewijk K (2005) Three centuries of global population growth: a spatial referenced population (density) database for 1700–2000. Popul Environ 26:343–367
- Klimo E, Hager H (eds) (2001) The floodplain forests in Europe. Koninklijke Brill NV, Leiden
- Kuhn K (2005) Die Kiesbänke des Tagliamento (Friaul, Italien). Ein Lebensraum für Spezialisten im Tierreich. Jahrbuch des Vereins zum Schutz der Bergwelt 70:37–44
- Lemke H, Löffler F, Fartmann T (2010) Habitat- und Nahrungspräferenzen des Kiesbank-Grashüpfers (*Chorthippus pullus*) in Südbayern. Articualta 25:133–149
- Lude A, Reich M, Plachter H (1999) Life strategies of ants in unpredictable floodplain habitats of Alpine rivers (Hymenoptera: Formicidae). Entomol Gen 24:75–91
- Machalett B, Oches EA, Frechen M, Zöller L, Hambach U, Mavlyanova NG, Marković SB, Endlicher W (2008) Aeolian dust dynamics in central Asia during the Pleistocene: driven by the long-term migration, seasonality, and permanency of the Asiatic polar front. Geochem Geophys Geosyst 9:Q08Q09, doi: 10.1029/2007GC001938
- Malmqvist B, Rundle S (2002) Threats to the running water ecosystems of the word. Environ Conserv 29:134–153
- Manderbach R, Framenau V (2001) Spider (Arachnida: Araneae) communities of riparian gravel banks in the northern parts of the European Alps. Bull Br arachnol Soc 12:1–9
- Martinet F, Dubost M (1992) Die letzen naturnahen Alpenflüsse. Versuch einer Bestandsaufnahme. CIPRA 11:11–60
- Messner B (1963) Beobachtungen zum Weidefraß und Galeriebau von *Tridactylus variegatus* Latr. (Saltatoria, Tridactylidae) in Bulgarien. Zool Anz 173:274–278
- Nickel H (1999) Life strategies of Auchenorrhyncha species on river floodplains in the northern Alps, with description of a new species: *Macropsis remanei* sp. n. (Hemiptera). Reichenbachia 33:157–169
- Nilsson C, Berggren K (2000) Alterations of riparian ecosystems caused by river regulation. Bioscience 50:783–792
- Paetzold A, Yoshimura C, Tockner K (2008) Riparian arthropod responses to flow regulation and river channelization. J Appl Ecol 45:894–903
- Poniatowski D, Fartmann T (2008) The classification of insect communities: lessons from orthopteran assemblages of semi-dry calcareous grasslands in central Germany. Eur J Entomol 105:659–671
- Poniatowski D, Fartmann T (2010) What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? J Insect Conserv 14:637–645
- Poniatowski D, Fartmann T (2011) Weather-driven changes in population density determine wing dimorphism in a bush-cricket species. Agr Ecosyst Environ 145:5–9
- Poniatowski D, Defaut B, Llucià-Pomares D, Fartmann T (2009) The Orthoptera fauna of the Pyrenean region—a field guide. Articulata, Beiheft 14:1–143
- Reich M (1991) Grasshoppers (Orthoptera, Saltatoria) on alpine and dealpine riverbanks and their use as indicators for natural floodplain dynamics. Regul River 6:333–339



- Robinson CT, Tockner K, Ward JV (2002) The fauna of dynamic riverine landscapes. Freshwater Biol 47:661–677
- Russ M (2006) Die Dreizehenschrecke Xya variegata Latreille, 1809,
   und die Grüne Strandschrecke Aiolopus thalassinus, Fabricius,
   1781—zwei bemerkenswerte Heuschreckenfunde im Lafnitztal
   (Orthoptera: Tridactylidae, Acrididae). Beitr Entomofaun
   7:154–157
- Sadler JP, Bell D, Fowles A (2004) The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. Biol Conserv 118:41–56
- Samways MJ (2005) Insect diversity conservation. Cambridge University Press, Cambridge
- Stefanescu C, Herrando S, Páramo F (2004) Butterfly species richness in the northwest Mediterranean Basin: the role of natural and human-induced factors. J Biogeogr 31:905–915
- Stelter C, Reich M, Grimm V, Wissel C (1997) Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper *Bryodema tuberculata*. J Anim Ecol 66:508–518
- Szijj J (1992) Ökologie der Heuschrecken in den Flussmündungen Griechenlands im Zusammenhang mit der landschaftsökologischen Entwicklung (Orthoptera, Saltatoria). Dtsch ent Z, N.F. 39:1–53
- R Development Core Team (2010) R: a language and environment for statistical computing. http://www.R-project.org. Accessed 18 December 2010
- Thorens P, Nadig A (1997) Verbreitungsatlas der Orthopteren der Schweiz. Laubheuschrecken, Grillen, Feldheuschrecken (Orthoptera), Gottesanbeterin (Mantodea). Doc Faun Helvetiae 16:1–236
- Tockner K, Stanford JA (2002) Riverine flood plains: present state and future trends. Environ Conserv 29:308–330

- Tockner K, Bunn SE, Gordon C, Naimann RJ, Quinn GP, Stanford JA (2008) Flood plains: critically threatened ecosystems. In: Polunin VNC (ed) Aquatic ecosystems. Trends and global prospects. Cambridge University Press, Cambridge, pp 45–61
- Tonolla D, Acuña V, Uehlinger U, Frank T, Tockner K (2010) Thermal heterogeneity in river floodplains. Ecosystems 13:727–740
- Villar L, Sesé JA, Ferrández JV (1997) Atlas de la Flora del Pirineo Aragonés. Vol. I. Instituto de Estudios Altoaragoneses y Consejo de Protección de la Naturaleza de Aragón, Huesca
- Villar L, Sesé JA, Ferrández JV (2001) Atlas de la Flora del Pirineo Aragonés. Vol. II. Instituto de Estudios Altoaragoneses y Consejo de Protección de la Naturaleza de Aragón, Huesca
- Ward JV, Bretschko G, Brunke M, Danielopol D, Gibert J, Gonser T, Hildrew AG (1998) The boundaries of river systems: the metazoan perspective. Freshwater Biol 40:531–569
- Ward JV, Tockner K, Schiemer F (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regul River 15:125–139
- Ward JV, Tockner K, Arscott DB, Claret C (2002) Riverine landscape diversity. Freshwater Biol 47:517–539
- Wenger EL, Zinke A, Gutzweiler K-A (1990) Present situation of European floodplain forests. Forest Ecol Manag 33(34):5–12
- Zechner L (2009) Gefleckte Grabschrecke *Xya variegata* Latreille, 1809. In: Zuna-Kratky T, Karner-Ranner E, Lederer E, Braun B, Berg H-M, Denner M, Bieringer G, Ranner A, Zechner L (eds) Verbreitungsatlas der Heuschrecken und Fangschrecken Ostösterreichs. Naturhistorisches Museum Wien, Wien, pp 152–153
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

