

Joint species models reveal the effects of environment on community assemblage of freshwater mussels and fishes in European rivers

Kentaro Inoue* , Katharina Stoeckl and Juergen Geist

Aquatic Systems Biology Unit, Department of Ecology and Ecosystem Management, Technical University of Munich, Mühlenweg 22, D-85354 Freising, Germany

ABSTRACT

Aim Given that riverine systems exhibit longitudinal environmental gradients from headwater to the mouth of a river, habitat heterogeneity appears to be a major driver of spatial variation in community composition among riverine localities. As freshwater ecosystems are amongst the most endangered ecosystems in the world, community-based conservation and multiple-species management are necessary to maintain ecosystem integrity. We used joint species distribution models (JSDMs) to investigate the relative importance of abiotic and biotic factors that are responsible for the distribution and co-occurrence of species in riverine ecosystems.

Location Central and northern Europe.

Methods We examined the general patterns of species assemblage of two endangered freshwater mussel species (*Margaritifera margaritifera* and *Unio crassus*) and their associated fish communities. We examined the patterns of positive or negative co-occurrence in mussel and fish species and identified shared abiotic responses between mussel–host pairs.

Results We found that the relative importance of abiotic and residual factors and patterns of significant species correlations varied among taxa: significant residual correlations were prevalent among fish species, whereas mussel occurrences were exclusively explained by abiotic factors. Mussels and their fish hosts generally had shared abiotic responses with some mismatched responses between mussel–host pairs.

Main conclusions Given that the composition of communities were tightly linked with abiotic factors and residual correlations, the results have significant implications for the conservation and restoration of aquatic communities. This study highlights the necessity to simultaneously consider environmental factors and species co-occurrences in the modelling of species distributions and assemblages of riverine communities. Such a holistic community conservation approach can reveal ecological similarities and differences among species, which can help us avoid conflicts among target-species conservation plans.

Keywords

aquatic community distribution and structure, community-based conservation, determinants of mussel distribution, joint species distribution model, latent variable model.

*Correspondence: Kentaro Inoue, Institute of Renewable Natural Resources, Texas A&M University, 1500 Research Parkway, College Station, TX 77843, USA.
E-mail: kentaro.inoue@ag.tamu.edu

INTRODUCTION

Understanding the underlying mechanisms that are responsible for species assemblage and distribution is a fundamental

goal of community ecology. Because species co-occurrence within any community is a product of various factors that work over ecological and evolutionary time-scales, numerous studies have been conducted to understand the rules behind

the assembly processes (sensu ecological assembly rules; Fox, 1999 for review). Two major hypotheses have been developed to explain species assemblages. The first is that the abiotic factors may act as a filter that restricts community membership to species that possess a particular set of functional traits (abiotic filtering; Keddy, 1992). The second is that biotic interactions may shape communities by limiting similarity among competing species that co-exist in particular communities (biotic filtering; MacArthur & Levins, 1967). While these are often tested independently by researchers, in reality the process of species assemblage is a function of complex interactions between abiotic and biotic filters (Araújo & Luoto, 2007; Kissling *et al.*, 2012) and other ecological forces, such as random speciation and extinction, limited dispersal, and ecological drift (Rosindell *et al.*, 2011).

Recent developments in analytical techniques allow us to assess the importance of abiotic factors and biological interactions that shape the current composition and distribution of communities. Species distribution models (SDMs) are pivotal tools for understanding the distribution of target species by associating observations of species occurrence with abiotic variables (Elith & Leathwick, 2009). Conceptually, these correlative SDMs are considered in the context of the Hutchinson's fundamental niche, a hypervolume in multivariate environmental space where populations of a species can maintain positive net growth rates (Pearman *et al.*, 2008; Kearney & Porter, 2009). However, biotic interactions are often left out of these basic SDM models or otherwise indirectly included by incorporating multiple single-species SDMs into one model (i.e. stacked SDM; Thuiller *et al.*, 2015). Comparing single-species SDMs that omit biotic interactions may lead to misleading conclusions that patterns of species co-occurrence (or exclusion) are primarily the results of similar (or dissimilar) habitat requirements and not from direct/indirect biotic interactions (e.g. competition, predation, disease; Ovaskainen *et al.*, 2010). Recently, a joint species distribution model (JSDM; sensu Pollock *et al.*, 2014) was developed to simultaneously explore interactions across many taxa and the response of species co-occurrence to abiotic variables (Warton *et al.*, 2015). The JSDM uses an extension of multivariate generalized linear mixed models (GLMM); it incorporates unmeasured abiotic and biotic factors (latent variables) that can explain variation in species composition not accounted for by measured predictor variables. In a conventional GLMM, the number of parameters increases quickly as the number of response variables (e.g. number of species) increase, which makes it difficult for the model to converge during model-fitting. Because the latent variables induce correlation between response variables and control model complexity, the JSDM enables us to analyse whole communities in a hierarchical and holistic manner within a single model (Warton *et al.*, 2015).

Local species assemblages in riverine ecosystems are strongly influenced by regional and local environmental conditions. River systems exhibit longitudinal gradients of physicochemical conditions from headwaters to the mouth

of a river (river continuum; Vannote *et al.*, 1980); therefore, spatial variation in community composition of biota is predicted to change gradually in accordance with changes in hydrologic and geomorphic properties (Benda *et al.*, 2004; Clarke *et al.*, 2008). Additionally, biotic interactions affect the composition of local communities. For example, predation pressure can alter the choice of microhabitat by prey species within streams, which leads to different assemblages being present in different stretches of a stream (Gilliam & Fraser, 2001). The interactions of abiotic and biotic filtering are further complicated when examining tightly coupled species, such as a host–parasite system. Obligate parasites have strong biotic interactions with their hosts, but also experience abiotic filtering directly or indirectly, via their host (Dybdahl & Storfer, 2003; Thrall *et al.*, 2007).

In this study, we used JSDMs to investigate the pattern of species assemblage and distribution in stream ecosystems by taking into account species responses to abiotic factors and biotic interactions. We focused on communities of freshwater mussels and fishes in central and northern European rivers. In recent years, freshwater mussels and fishes have received growing awareness of the need for conservation and sustainable fisheries due to severe declines in their populations across Europe (Fausch *et al.*, 2002; Lopes-Lima *et al.*, 2016). Furthermore, freshwater mussels (Bivalvia: Unionoida) are obligate parasites of freshwater fish during their larval stage, where the larvae (known as glochidia) metamorphose into free-living juveniles. The degree of host specificity in individual mussel species varies from generalists to specialists; the assemblage of fish species in a community and the distribution of fish hosts may strongly influence the distribution of freshwater mussels, especially for host-specialists (Schwalb *et al.*, 2011). Therefore, the findings of JSDMs are useful not only to understand the relative importance of abiotic and biotic factors that are responsible for the distribution and co-occurrence of species, but also to effectively develop community-based conservation and fisheries management in order to maintain productivity and ecosystem integrity.

We focused on two imperilled mussel species, *Margaritifera margaritifera* (freshwater pearl mussel) and *Unio crassus* (thick-shelled river mussel), and their associated fish communities. These mussel species were chosen because the biology of the species has been relatively well studied, including their reproductive biology (Young & Williams, 1984; Taeubert *et al.*, 2012b) and habitat requirements (Hastie *et al.*, 2000; Geist & Auerswald, 2007; Geist, 2010; Denic *et al.*, 2014; Stoeckl & Geist, 2016). Although the two species have a broad distribution across central and northern Europe and co-occur in some parts, they have different reproductive modes and habitat preferences. *Margaritifera margaritifera* is a host-specialist and uses two salmonid species in Europe (*Salmo salar* and *S. trutta*; Young & Williams, 1984; Geist *et al.*, 2006), while *U. crassus* is a host-generalist and uses more than 10 fish species including one of the hosts for *M. margaritifera* (*S. trutta*; e.g. Taeubert *et al.*, 2012b;

Stoeckl *et al.*, 2014). Furthermore, *M. margaritifera* often occupies cold, oligotrophic streams (habitat-specialist; Geist, 2010), whereas *U. crassus* occupies a wide variety of flows, sediment types and water conditions (habitat-generalist; Stoeckl & Geist, 2016). Currently these species are listed as endangered by the International Union for Conservation of Nature (IUCN); despite the differences in their life history and habitat preference, the conservation efforts for these species are often combined into a single management plan.

The goal of this study was to identify the general patterns of species assemblage in mussel and fish communities and whether abiotic factors or biotic interactions are responsible for structuring these communities. Our three objectives were to examine (1) the patterns of positive or negative co-occurrence in mussel and fish species, (2) how well abiotic factors predict community composition and (3) the patterns of shared abiotic responses between mussel–host pairs. Given that the recruitment of *M. margaritifera* populations is strongly linked with abiotic stream conditions (Geist & Auerswald, 2007) and the availability of its fish hosts (Geist *et al.*, 2006), we predicted that the presence of *M. margaritifera* is a function of both abiotic factors and biotic interaction with its hosts. Because the recruitment of *U. crassus* populations strongly depends on the density of fish hosts (Stoeckl *et al.*, 2014) and this species is highly tolerant to a wide range of stream conditions (Stoeckl & Geist, 2016), we predicted that *U. crassus* is strongly affected only by the presence of its fish hosts.

METHODS

Community data

We obtained occurrence records for *M. margaritifera*, *U. crassus*, and fish species across central and northern European streams from primary literature (Geist *et al.*, 2006; Taeubert *et al.*, 2012b; Stoeckl *et al.*, 2014; Lamand *et al.*, 2016) and technical reports (Stoeckl & Bayerl, 2016). In these studies, fish communities were sampled quantitatively by electrofishing adjacent to mussel aggregations. One study conducted repeated sampling over several years to ensure the reliability of sampling efforts (Geist *et al.*, 2006). This study showed that fish species richness and density did not vary significantly between years. Because each study used different abundance measurements [e.g. presence/absence (Geist *et al.*, 2006), density (Geist *et al.*, 2006; Stoeckl *et al.*, 2014) and count (Taeubert *et al.*, 2012b; Lamand *et al.*, 2016; Stoeckl & Bayerl, 2016)], we converted occurrence records into presence/absence data. Of 31 fish species initially obtained, we removed nine fish species due to a low number of occurrences ($n < 5$) and thus included 22 fish species from nine families in our analyses (Table 1).

Abiotic covariates

The distribution of mussels and fishes can be influenced by a range of abiotic factors, including variability in climate

Table 1 List of mussel and fish species obtained from primary literature and technical reports.

Species	Family	Ranking		
		MarMar	UniCra	Used
Mussels				
<i>Margaritifera margaritifera</i>	Margaritiferidae	n.a.	n.a.	x
<i>Unio crassus</i>	Unionidae	n.a.	n.a.	x
Fish				
<i>Abramis brama</i>	Cyprinidae	5	9	x
<i>Alburnoides bipunctatus</i>	Cyprinidae	5	7 [†]	x
<i>Alburnus alburnus</i>	Cyprinidae	5	9 [†]	x
<i>Anguilla anguilla</i>	Anguillidae	5	9	x
<i>Barbatula barbatula</i>	Nemacheilidae	5	9	x
<i>Barbus barbus</i>	Cyprinidae	5	4 [†]	x
<i>Chondrostoma nasus</i>	Cyprinidae			
<i>Cottus gobio</i>	Cottidae	1	21*	x
<i>Cyprinus carpio</i>	Cyprinidae			
<i>Esox lucius</i>	Esocidae	5	9	x
<i>Gasterosteus aculeatus</i>	Gasterosteidae	22	1*	x
<i>Gobio gobio</i>	Cyprinidae	5	6	x
<i>Gymnocephalus cernua</i>	Percidae			
<i>Lampetra planeri</i>	Petromyzontidae	2	20	x
<i>Leuciscus leuciscus</i>	Cyprinidae	5	8 [†]	x
<i>Lota lota</i>	Lotidae	5	9	x
<i>Oncorhynchus mykiss</i>	Salmonidae	5	9	x
<i>Perca fluviatilis</i>	Percidae	5	9 [†]	x
<i>Phoxinus phoxinus</i>	Cyprinidae	21	3*	x
<i>Pseudorasbora parva</i>	Cyprinidae	5	9 [†]	x
<i>Rhodeus amarus</i>	Cyprinidae			
<i>Rutilus rutilus</i>	Cyprinidae	5	9 [†]	x
<i>Salmo trutta</i>	Salmonidae	3*	22 [†]	x
<i>Scardinius erythrophthalmus</i>	Cyprinidae			
<i>Silurus glanis</i>	Siluridae	20	2	x
<i>Squalius cephalus</i>	Cyprinidae	5	5*	x
<i>Thymallus thymallus</i>	Salmonidae	4	9	x
<i>Tinca tinca</i>	Cyprinidae		*	

n.a., not applicable.

Two mussel and 22 fish species were used in the analyses (the number of occurrence points > 5; 'x' in Used column). The rankings that how abiotic responses of fish are similar to *Margaritifera margaritifera* (MarMar) and *Unio crassus* (UniCra) are given for each fish species. Host status is shown in the primary host (*) and the secondary host (†) based on laboratory and field studies (Young & Williams, 1984; Doua *et al.*, 2012; Taeubert *et al.*, 2012a,b; Stoeckl *et al.*, 2014; Lamand *et al.*, 2016).

(Inoue *et al.*, 2015), heterogeneity in riparian land cover (Morris & Corkum, 1996; Österling & Högberg, 2014) and variability in hydrology and geology (Strayer, 1993). Temperature and precipitation can be key factors determining fundamental niches for aquatic organisms (Heino *et al.*, 2009).

Therefore, we obtained four bioclimatic variables, including isothermality, annual temperature range ($^{\circ}\text{C}$), total precipitation (mm yr^{-1}) and precipitation seasonality, from WorldClim (<http://www.worldclim.org>; Hijmans *et al.*, 2005). We also obtained the amount of yearly evapotranspiration (mm yr^{-1}), which is the effective quantity of water that is removed from the soil due to evaporation and transpiration processes, from CGIAR-CSI (<http://www.cgiar-csi.org>).

Current declines in mussel and fish populations are mostly caused by habitat destruction and degradation. While habitat destruction and severe point-source pollution may cause immediate impact on the distribution of aquatic organisms, sediment erosion and diffuse pollution associated with land use in riparian zone have the potential to affect aquatic organisms and their habitat (Brim-Box & Mossa, 1999). In particular, cropland and pastureland reduce infiltration rates and increase run-off, erosion, nutrient loads and siltation (Denic & Geist, 2015). Therefore, we obtained the proportion of cropland (land used for the cultivation of food) and pastureland (land used to support grazing animals) from the NASA Socioeconomic Data and Application Center (SEDAC; <http://sedac.ciesin.columbia.edu>).

Finally, we obtained the other variables that characterize water quality, stream size and catchments. Due to a lack of consistent hydrological data across Europe, we were able to use four variables: the estimated phosphate concentration (equilibrium PO_4^{3-} concentration) in rivers, mean elevation (m) and slope (%) in a primary catchment defined by the River and Catchment Database (Vogt *et al.*, 2007) and the Strahler stream order obtained from the European Commission's JRC Water Portal (<http://water.jrc.ec.europa.eu/>) and JRC Catchment Characterisation and Modelling (<http://ccm.jrc.ec.europa.eu/>). Phosphorus is a major limiting nutrient in freshwater and is often responsible for causing eutrophication (Schindler *et al.*, 2008). Because the equilibrium PO_4^{3-} concentration is estimated based on local lithology, we considered the PO_4^{3-} concentration as the natural level of phosphate in stream systems. Furthermore, because the Strahler stream order increases in hierarchical fashion from headwaters to the mouth of a river, we considered the stream order as a surrogate for the relative size and natural differences in physical conditions of rivers (Hughes *et al.*, 2011).

We recorded the point estimate of abiotic variables at each sampled site (resolution of 5×5 km). To reduce spatial autocorrelation among sampled sites, we considered each stream segment in the primary catchment as a single community (mean length of stream segments = 6939 m; mean area of catchments = 22.5 km^2). When multiple records from the same primary catchment were available, we took the average of each abiotic variable and combined the species occurrence records into a single record (mean number of sites per stream segment = 1.29 sites). As a result, we included 70 communities in eight major river drainages across central and northern Europe (Fig. 1). We initially obtained a total of 11 abiotic variables at each sampled site (Table 2). Prior to the analyses, we tested for

multicollinearity among the abiotic variables (Pearson correlation coefficient < 0.6); we used eight uncorrelated abiotic variables for further analyses (Table 2).

Joint species distribution modelling

We used BORAL package (Hui, 2016) in R v3.2.3 (R Core Team, 2015) to investigate patterns of species co-occurrence while considering abiotic responses and biotic interactions. Briefly, BORAL incorporates latent variables derived from Bayesian Markov chain Monte Carlo (MCMC) estimation to model correlations between species with and without covariates (i.e. abiotic variables; Hui, 2016). If covariates are not used, BORAL fits a pure latent variable model (LVM) in which species occurrence data are regressed against the latent variables (Hui *et al.*, 2015; Hui, 2016). The latent variables for each site can be used as a pair of axes to construct an unconstrained ordination, and the corresponding species-specific coefficients can be added to the ordination as a biplot for visualizing how species composition differs across sites (Hui *et al.*, 2015). With covariates, BORAL fits a correlated response model (CRM) that combines separate species generalized linear models with the abiotic covariates along with latent variables. Because correlation between species co-occurrence can be due to species' abiotic responses and/or other residual correlations (e.g. unknown abiotic variables, biotic interactions; Warton *et al.*, 2015), the latent variables in the CRM can be interpreted as variables accounting for any residual covariation not explained by the abiotic covariates (Hui, 2016). Therefore using the latent variables for each site, we were able to construct a residual ordination that represents site and species patterns after controlling for abiotic effects. Furthermore, the CRM allowed us to separate the correlations between species due to abiotic response and the residual correlations. This enabled us to assess the direction (+/−) and the strength of correlations between species due to the abiotic response and the residual correlations.

First, we used species occurrence data only to fit a LVM with two latent variables and constructed an unconstrained biplot to visualize site and species patterns. We then added abiotic covariates in a CRM to construct a residual biplot after controlling for the effect of abiotic variables. From the CRM, we also examined the sign and the strength of significant correlations between species co-occurrence due to abiotic response and the residual correlations, as based on the 95% credible intervals excluding zero. Furthermore, by taking a proportional difference in the trace of the estimated residual covariate matrix between the LVM and CRM, we determined how much of species co-occurrence is explained by abiotic covariates (Warton *et al.*, 2015; Hui, 2016).

We further identified the relative importance of abiotic covariates for each species and examined shared abiotic response between mussels and their fish hosts by comparing estimated coefficients for each abiotic covariate. We categorized fish hosts into 'primary' and 'secondary' hosts based on previous findings from laboratory and field studies (Table 1;

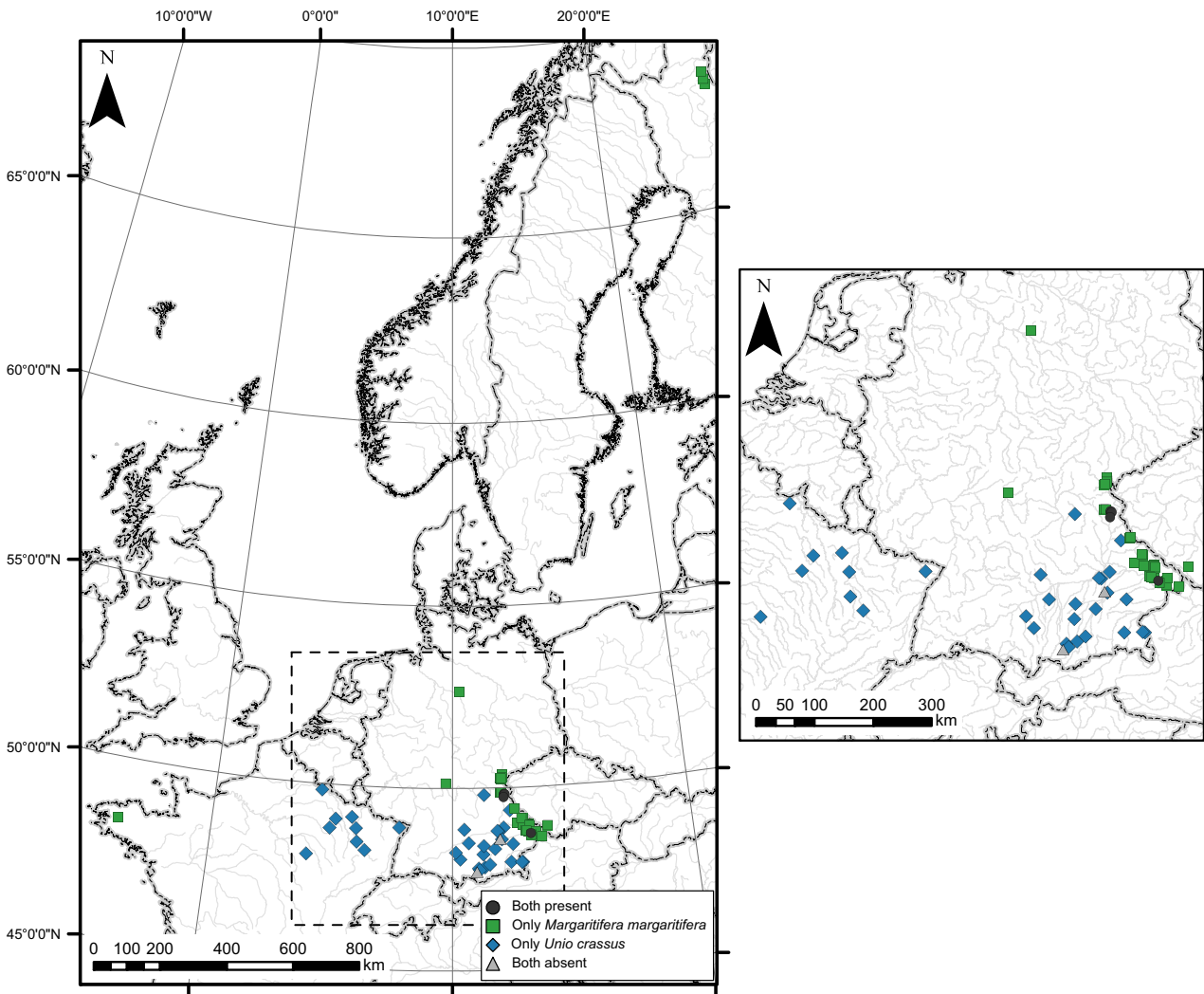


Figure 1 Map of central and northern Europe indicating sites where mussels and fish communities were sampled. Coloured dots represent the presence of mussel species (circles = both mussel species are present; squares = only *Margaritifera margaritifera* is present; diamonds = only *Unio crassus* is present; triangles = both mussel species are absent). The magnified inset map (right) shows central European sampling locations (dotted lines). [Colour figure can be viewed at wileyonlinelibrary.com]

Young & Williams, 1984; Douda *et al.*, 2012; Tæubert *et al.*, 2012a,b; Stoeckl *et al.*, 2014; Lamand *et al.*, 2016). We plotted the posterior median coefficients for each abiotic covariate with 95% credible interval to determine shared abiotic responses between mussels and their fish host. Furthermore, based on pairwise correlations between mussel and fish species due to abiotic response from the CRM, we examined how abiotic responses of fish species were similar to *M. margaritifera* and *U. crassus*. We ranked each fish species, where the highest rank was given to a fish species that had the most positive correlation with the mussel species.

We ran each model for 300,000 iterations with the first 200,000 discarded as burn-in and the remaining samples thinning by a factor of 100, and thus, 1000 samples were retained for analysis. For both LVM and CRM, we used the Bernoulli distribution for the overdispersion parameter, no site effects and the default priors for MCMC parameters.

Model convergence was checked via BORAL diagnostic tools using Dunn–Smyth residuals and normal quantile plot of residuals.

RESULTS

We verified the convergence of MCMC for all models (see Fig. S1 and S2 in Supporting Information). The JSDMs revealed that the patterns of species co-occurrence in central and northern European rivers were largely attributed to abiotic factors and latent variables (Fig. 2). An unconstrained ordination under the LVM showed high variability in sampled sites, where sites were clustered into two groups: sites with exclusive occurrence of *M. margaritifera* and *U. crassus* (Fig. 2a). Corresponding to the ordination plot, the species biplot showed three clusters of species along the two latent variables (Fig. 2a). A cluster of *M. margaritifera* and three

Table 2 Abiotic covariates used in joint species distribution models (JSDMs). Of 11 bioclimatic, land use and other abiotic variables initially examined, eight uncorrelated covariates were chosen for JSDMs (Pearson correlation coefficient < 0.6; 'x' in the Used column).

Covariates	Description	Resolution	Used
Climate variables			
Isothermality	Proportion of temperature difference between mean daily range and annual range	1 km	
Annual temperature range (°C)	Temperature range between coldest and warmest	1 km	x
Annual precipitation (mm)	Total annual precipitation	1 km	x
Precipitation seasonality	Coefficient of precipitation variation	1 km	
Actual evapotranspiration (mm yr ⁻¹)	Effective quantity of water that is removed from the soil due to evaporation and transpiration processes	1 km	
Land use variables			
Area of cropland (%)	Proportion of land areas used as cropland (land used for the cultivation of food) in the year 2000	5 km	x
Area of pasture (%)	Proportion of land areas used as pasture land (land used to support grazing animals) in the year 2000	5 km	x
Other abiotic variables			
Stream order	Strahler stream order	Catchment	x
PO ₄ ³⁻ concentration (mg L ⁻¹)	Estimated equilibrium phosphate concentration in rivers based on local lithology	5 km	x
Elevation (m)	Average elevation in the primary catchment	Catchment	x
Slope (%)	Average slope in the primary catchment	Catchment	x

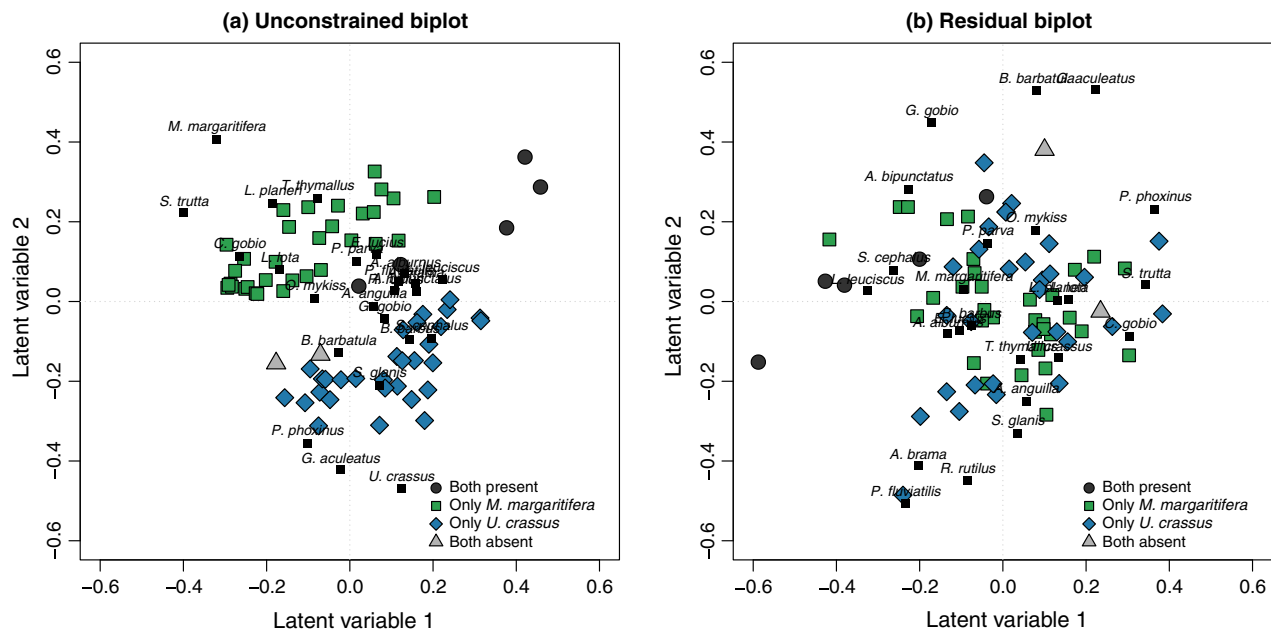


Figure 2 Unconstrained ordination based on the latent variable model (LVM; (a)) and residual ordination based on the correlated response model (CRM; (b)) constructed from the latent variables for each sampled site. Colours represent the presence of mussel species: (circles = both mussel species are present; squares = only *Margaritifera margaritifera* is present; diamonds = only *Unio crassus* is present; triangles = both mussel species are absent). Biplots (small squares) are based on the species-specific coefficients for the latent variables; 24 mussel and fish species with the largest factor loading from the origin are shown. Species in the same direction and far from the origin are highly correlated. [Colour figure can be viewed at wileyonlinelibrary.com]

fish species (*Lampetra planeri*, *S. trutta* and *Thymallus thymallus*) was negatively associated with the first latent variable, and positively associated with the second latent

variable. A cluster of *U. crassus* and three fish species (*Gasterosteus aculeatus* and *Phoxinus phoxinus*) was negatively associated with the second latent variable. Finally, a cluster

of 12 fish species was positively associated with the first latent variables; however, the association was rather weak (Fig. 2a). These clusters indicate that the presence of the mussel species and some of their host species (e.g. *M. margaritifera* and its host *S. trutta*; *U. crassus* and its hosts *G. aculeatus* and *P. phoxinus*) are highly correlated and that these correlations are likely due to shared abiotic preferences.

After controlling for the abiotic factors under the CRM, a residual ordination showed less variability among sites and clusters of species were less pronounced (Fig. 2b). These indicate that site characteristics and species correlations are likely derived from abiotic conditions; most of sites and species clustered around the origin (Fig. 2b). However, a few species departed from the origin *Cottus gobio*, *P. phoxinus* and *S. trutta* were positively associated with the first latent variable while a few cyprinid fish species (*Alburnoides bipunctatus*, *Leuciscus leuciscus* and *Squalius cephalus*) were negatively associated with the first latent variable; a cluster of fish species (*Abramis brama*, *Rutilus rutilus* and *Perca fluviatilis*) was negatively associated with the second latent variable and three fish species (*B. barbatula*, *G. aculeatus* and *Gobio gobio*) were positively associated with the second latent variables (Fig. 2b). Based on the trace of covariance matrices, the inclusion of abiotic covariates reduced the trace from 92.0 to 80.1. Thus, abiotic factors explained approximately 12.9% of the variation in overall mussel and fish communities.

Using the CRM, we estimated correlations between species due to abiotic response and the residual correlations (Fig. 3). We found a small number of significant correlations between species due to a shared abiotic response (Fig. 3a) relative to

the residual correlations (Fig 3b). We found similar numbers of significant positive and negative correlations between species due to their abiotic response, in which approximately 30% of correlations were between mussel and fish species (14 of 62 positive correlations and 11 of 21 negative correlations, respectively; Fig. 3a). In particular, a strong, negative correlation was found between *M. margaritifera* and *U. crassus*, indicating that these species likely occupy different environmental space and have different habitat requirements. Interestingly within the significant correlations, the mussel species and their host species generally had significantly strong, positive correlations (e.g. *M. margaritifera* and *S. trutta*; *U. crassus* and *G. aculeatus*, *P. phoxinus* and *S. cephalus*); however, this was not the case between *U. crassus* and *C. gobio/S. trutta* (Table 1; Fig. 3). Most of the correlations of mussel with fish showed opposite correlations between *M. margaritifera* and *U. crassus* (e.g. positive correlation of *S. trutta* with *M. margaritifera*, but negative correlation with *U. crassus*).

The residual correlations were dominated by a large number of positive correlations (75 positive and five negative correlations, respectively; Fig. 3b). The presence of the two mussel species was not significantly correlated with any fish species. Within the significant correlations, a majority of positive correlations was found within cyprinid species (29 of 75 positive correlations); most of the negative correlations were involved with the headwater species *P. phoxinus*, where it had strong, negative correlations with *A. brama*, *Anguilla anguilla*, *P. fluviatilis* and *R. rutilus*, which are more common in the lower stretches of a river with slow current.

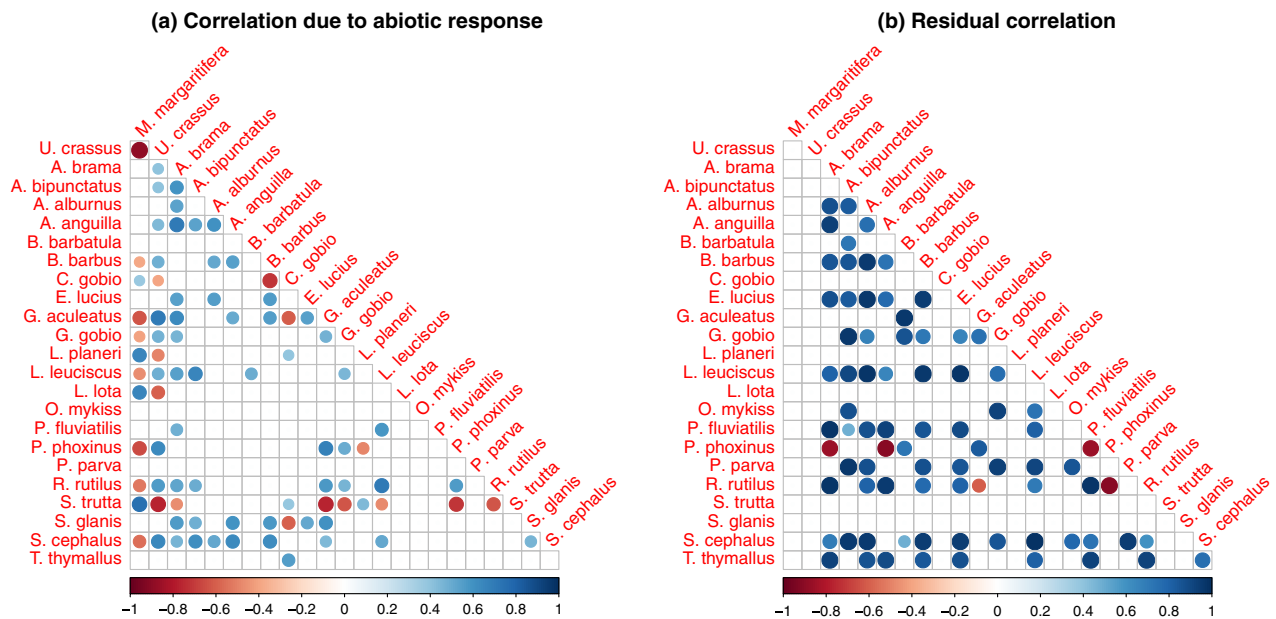


Figure 3 Plots of the correlations between species due to abiotic responses (a) and residual correlations (b) based on the correlated response model (CRM). Only significant correlations, based on 95% credible intervals excluding zero, are shown. Colour gradients (from red to blue) represent negative and positive correlations, respectively. The strength of correlations is presented by the size of the circles. [Colour figure can be viewed at wileyonlinelibrary.com]

Several species had no significant correlations with any other species (e.g. *C. gobio*, *L. planeri*, *Lota lota*, *S. trutta* and *Silurius glanis*).

Using the median coefficients for each abiotic covariate, we identified the relative importance of abiotic covariates for each species and between mussel and its hosts (Fig. 4). *Margaritifera margaritifera* had significantly negative associations with PO_4^{3-} concentration and cropland, whereas *U. crassus* had significantly positive associations with these abiotic variables. These indicate that *M. margaritifera* likely occurs in naturally oligotrophic streams with less agricultural activities in the surrounded landscape, while *U. crassus* likely occurs in naturally meso- to eutrophic streams in agricultural landscape. Furthermore, *M. margaritifera* had significantly negative association with slope of catchments. Similar trends in significant associations with abiotic variables were found in host species (Fig. 4); however, we found several mismatched associations between the mussel and its hosts and between host statuses (i.e. primary vs. secondary hosts). For example, while *M. margaritifera* had significant negative associations with cropland and slope, *S. trutta* did not have significant

association with these covariates (Fig. 4). Despite the mismatch, based on the ranking by similarity in abiotic responses, *S. trutta* occupies similar environmental space to *M. margaritifera* (Table 1). Such mismatches were more evident in *U. crassus* and its hosts. In general, the primary hosts had similar trends in associations to *U. crassus* relative to the secondary hosts (Table 1 and Fig. 4); however, significant departure was observed in *C. gobio*, whose abiotic response was greatly divergent from *U. crassus* (Table 1).

DISCUSSION

Generally in riverine ecosystems, species sorting by abiotic filtering is a major driver for structuring community compositions at a regional scale, and biotic interactions are a potential filter on local community composition after species have passed through the physicochemical habitat filters (Poff & Allan, 1995; Poff, 1997; Marchetti & Moyle, 2001). However, many studies often failed to simultaneously include biotic interactions among coexisting species (Ovaskainen *et al.*, 2010). In this study, we demonstrated the use of JSDMs and

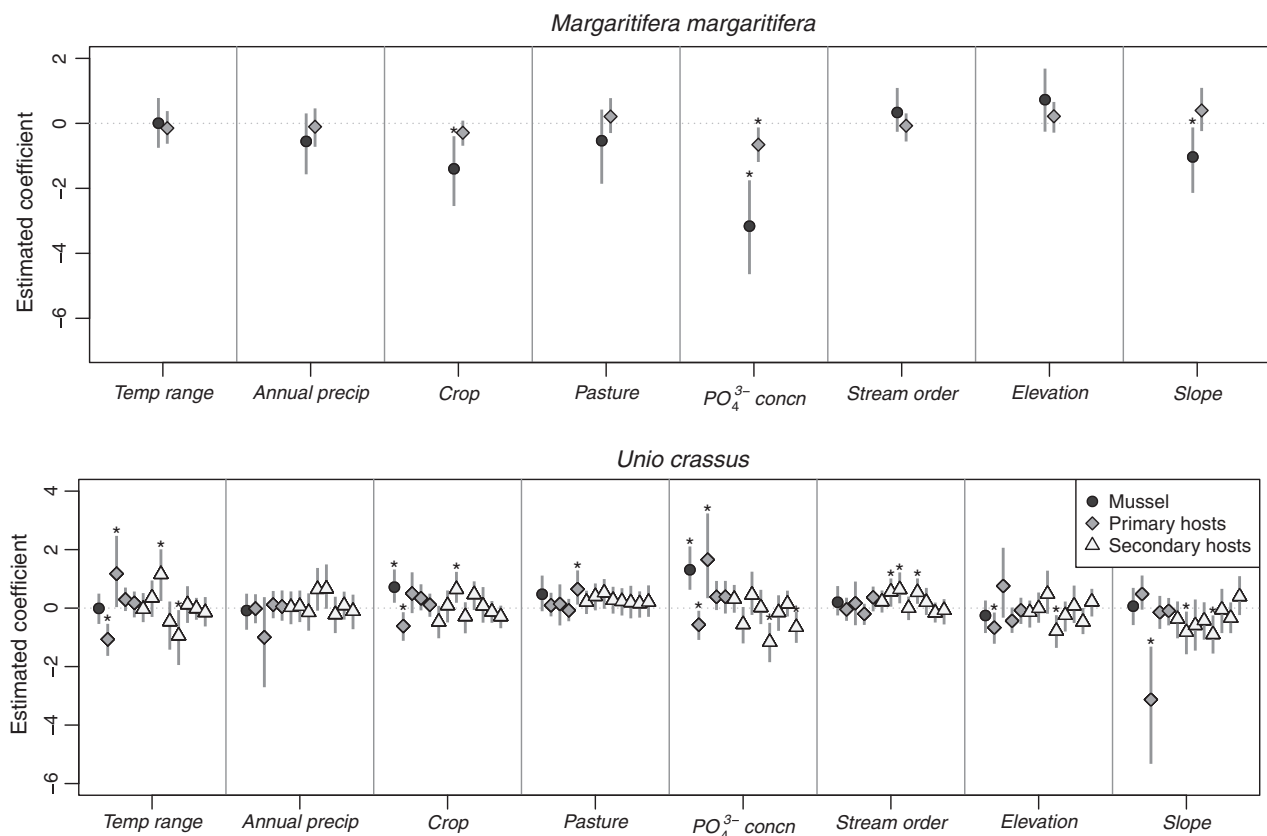


Figure 4 Estimated coefficients of six abiotic covariates for *Margaritifera margaritifera* (top) and *Unio crassus* (bottom) based on the correlated response model (CRM). Points are the posterior median coefficients and grey lines associated with the points present 95% credible intervals. For each mussel species, coefficients of its primary (grey diamonds) and secondary hosts (light grey triangles) are shown. *Margaritifera margaritifera* has only one primary host: *Salmo trutta*; *U. crassus* has 12 primary and secondary hosts (from left to right: *Cottus gobio*, *Gasterosteus aculeatus*, *Phoxinus phoxinus*, *Squalius cephalus*, *Alburnoides bipunctatus*, *Alburnus alburnus*, *Barbus barbus*, *Leuciscus leuciscus*, *Perca fluviatilis*, *Pseudorasbora parva*, *Rutilus rutilus*, *S. trutta*). Asterisks (*) represent the estimate coefficients are significantly different from zero.

found that the co-occurrence of mussel and fish communities in central and northern Europe was complexly interacted with abiotic covariation and residual correlations (Figs 2 and 3). However, the relative importance of abiotic and residual factors and patterns of significant correlations among species varied among taxa: significant residual correlations were prevalent among fish species, whereas mussel occurrences, despite their parasitic phase during the larval stage, were exclusively explained by abiotic factors.

Although the two mussel species co-occur in some parts of their distributions, they frequently occupy different habitats. This pattern was further demonstrated in our results with communities being sorted into *M. margaritifera*-sites and *U. crassus*-sites (Fig. 2). *Margaritifera margaritifera* and *U. crassus* responded oppositely to levels of PO_4^{3-} concentration in rivers and proportions of cropland surrounding rivers, both of which are indicative of water quality (Fig. 4). Our results support the previous findings that *M. margaritifera* has a strong preference to low levels of natural phosphate concentration in undisturbed landscape (Geist & Auerswald, 2007; Geist, 2010), while *U. crassus* can tolerate high levels of nutrient and is likely able to persist in disturbed stream systems (Denic *et al.*, 2014; Stoeckl & Geist, 2016). Furthermore, the negative relationship of *M. margaritifera* with slope corresponds to a previous study of *M. margaritifera* in Northern Ireland (Wilson *et al.*, 2011). Given that *M. margaritifera* tends to inhabit in a sediment matrix containing fine gravels and large boulders (Quinlan *et al.*, 2015), it was hypothesized that dynamic flow in high slope habitats may make substrate unstable, which increases the risk of mussels being washed out. Interestingly, the presence of fish hosts does not likely predict mussel presence river-wide, indicating that abiotic conditions are primary factors to explain the co-occurrence of mussels and their fish hosts within a given river (Fig. 3). In general, mussels and their fish hosts had shared abiotic responses (Fig. 4); however, there were some mismatches of shared abiotic responses between mussel–host pairs. For instance, *S. trutta* was not sensitive to proportion of croplands surrounding rivers. A previous study reported that *S. trutta* tend to have lower densities in functionally intact *M. margaritifera* populations (i.e. with recent reproduction of *M. margaritifera*) relative to those populations with no recent recruitment (Geist *et al.*, 2006). The results of this study coupled with the previous findings suggest that *M. margaritifera* is more sensitive to eutrophication than its fish host. For *U. crassus*, none of the 12 potential host fishes used in this study had a perfect match of abiotic responses. Generally, *U. crassus* and its primary hosts had more similar abiotic responses than those of the secondary hosts; however, *C. gobio*, which was identified as a primary host in northeastern France (Lamand *et al.*, 2016), happens to have one of the most dissimilar responses to the abiotic variables. Previous studies showed that *U. crassus* may not use the same hosts across their range (Douda *et al.*, 2012; Taeubert *et al.*, 2012b). Given that functional *U. crassus* populations are often found with high densities of

primary hosts (Stoeckl *et al.*, 2014), our results and previous studies suggest that *U. crassus* may take advantage of their tolerance to a wide range in abiotic conditions to use locally abundant fish host species.

In contrast to freshwater mussels, fish community composition was a function of species' responses to both the abiotic and residual variables, with a large number of positive residual correlations (Fig. 3). All fish species in this study, including two non-native species (*Oncorhynchus mykiss* and *Pseudorasbora parva*), are widely distributed across central and northern Europe. Our results suggest that community compositions of such widespread species are less influenced by the abiotic covariates in this study, but are likely more enhanced by the influence of abiotic factors that were not included in this study and/or species interactions. At a local community scale, predation by fish is known to be a dominant factor to determine species composition (Jackson *et al.*, 2001). Occurrences of predatory and piscivorous species such as *A. anguilla* and *Esox lucius* had strong positive correlations with prey species (e.g. *A. brama*, *P. fluviatilis* and *R. rutilus*), supporting the expectation that the presence of prey species is one indicator of habitat suitability for predators. Some fish species (e.g. *C. gobio*, *L. planeri*, *L. lota*, *S. trutta* and *S. glanis*), on the other hand, have strong correlations of co-occurrence due to abiotic response, but no residual correlations. These species are all known to occur in cold, well-oxygenated streams with gravel and cobble substrates needed for spawning (Kottelat & Freyhof, 2007), suggesting that shared habitat preferences are primary factors for their co-occurrence.

We note that because the residual correlations were induced from the latent variables, these correlations could be derived from any predictors that we did not include in the models and/or biotic interactions. In our JSDMs, we included abiotic variables that potentially influence the distributions of mussels and fishes. However, given that a large number of species correlations among fishes were from residual correlations, further study incorporating additional abiotic/biotic factors is needed to elucidate the association between species co-occurrences and biological interactions in fish communities. These include characteristics of microhabitats and physicochemical conditions, hydraulic conditions, species' traits and behaviour, and interactions with other species not included in our analyses. Furthermore, we used presence/absence data in our JSDMs. Obtaining true absence data are often problematic because absence can include the true absence and failure to detect a species' presence in an occupied habitat. Imperfect detection is known to substantially reduce the predictive accuracy of SDMs (Lahoz-Monfort *et al.*, 2014). Given the impact of a lack of true absence in conventional SDMs, imperfect detection may influence the results of JSDMs. Future studies require investigating the sensitivity of a lack of true absence to JSDMs.

In general, host fish distributions are considered to be one of the most important dimensions of the fundamental niche for freshwater mussels (Haag & Warren, 1998). Despite their

close relationships with fish hosts, however, researchers have failed to predict mussel distributions solely based on host fish distributions (e.g. Bauer *et al.*, 1991). Mussels are often able to occupy a wide range of microhabitats as metamorphosed juveniles drop off fish hosts in an opportunistic fashion; however, growth and reproduction may only be optimized under favourable environmental conditions (Vaughn & Taylor, 2000). This study found that significant correlations between mussel–host pairs due to the abiotic factors, but some mismatches in abiotic responses as well as no evidence of residual correlations. Based on the results, we hypothesize that mussel distributions are nested within the host fish distributions and that the presence of fish hosts in given communities is driven by both abiotic and biotic factors, while the presence of mussels is primarily driven by local abiotic conditions. Previous studies with a single-species SDM partially supported this hypothesis, where the breadth of suitable habitats for fish hosts were larger than that of mussels (Inoue *et al.*, 2015) and the abundance of fish hosts as a predictor improved the model fitness of SDMs (Lois *et al.*, 2015).

Because the present study revealed that the composition of communities was tightly linked with abiotic factors and residual correlations, our results may have significant implications for the conservation and restoration of aquatic communities in European rivers and elsewhere. Because of drastic declines in populations of freshwater mussels in Europe, there have been vigorous conservation efforts devoted to the restoration of freshwater mussel habitats across European nations (e.g. projects funded by the EU LIFE Programme; Lopes-Lima *et al.*, 2016). Most conservation projects often focus on the conservation of a single mussel species and, by necessity, its fish host (i.e. target-species conservation), or the conservation of multiple mussel species within the same projects (i.e. target-taxon conservation). Conversely, the conservation of fish species often put much emphasis on a few economically and recreationally important species such as salmonids without considering other taxa (Geist, 2015). However, given the evidence of mismatches in abiotic responses and significant residual correlations among fish species, conservation and restoration planning can become more effective if they consider differences, as well as similarities, in habitat requirements among species in a community. Accordingly, we propose a holistic community conservation approach instead of target-species conservation programs to avoid conservation conflicts among species. For example, conservation and habitat restoration plans for *M. margaritifera* should be coupled with *L. planeri* (locally imperilled in the Danube River drainage) and *S. trutta* (a target species for conservation in fisheries) as evident from their similar environmental requirements. In contrast, given wide-ranging suitable hosts, conservation actions for *U. crassus* should take into account the local habitat conditions and the associated fish communities to maximize the success of population recovery. In the light of the increasing efforts into aquatic habitat restoration, there is a strong need to make habitat rehabilitation projects more efficient (Geist &

Hawkins, 2016). One way to achieve this is by identifying restoration sites based on the interactions between target species of conservation, as demonstrated here for the interaction between mussels and their fish hosts. As evident in the example of *M. margaritifera*, the findings that cropland and slope are important determinants of the species presence are of great value to stakeholders charged with minimizing the effect of land development on aquatic habitat and maximizing the efficiency of selecting potential habitats for reintroduction (Gum *et al.*, 2011). Finally, caution is warranted in basing target-taxon conservation efforts focusing both *M. margaritifera* and *U. crassus* within the same areas. Given that the two mussel species require different ecological niches, conservation approaches for both species should follow different habitat restoration targets and include the associated fish communities as identified herein.

We demonstrated that while community composition depends on complex interactions between species and their environment, the relative importance of abiotic and biotic factors is likely taxon-specific. We found that abiotic filtering is evident in the occurrence of freshwater mussels, while the composition of fishes in a community is complexly interacted with abiotic filtering and residual factors. We also found that joint models of community assemblage may be more appropriate for understanding mussel–host interactions and thus useful for developing effective species recovery and habitat restoration planning. Our results highlight the necessity to simultaneously consider abiotic variables and species co-occurrences in the modelling of species distributions, and ultimately in defining conservation and restoration targets.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Plots for residual analysis from a pure latent variable model (LVM).

Figure S2 Plots for residual analysis from a correlated response model (CRM).

BIOSKETCHES

Kentaro Inoue is a research scientist at Texas A&M University. He works with evolution and conservation of freshwater molluscs. His research focuses on understanding spatio-temporal patterns of biodiversity in response to environmental changes and the processes that promote and assemble diversity.

Katharina Stoeckl did her PhD on the ecology of the thick-shelled river mussel and is currently a postdoctoral researcher at Technical University of Munich. She works at the Coordination Office for Freshwater Mussels in the State of Bavaria, Germany. She is interested in the conservation of endangered mussels based on aut- and synecological aspects.

Juergen Geist is a professor of aquatic systems biology at Technical University of Munich. His primary research interest lies in understanding the functional processes in aquatic ecosystems that govern biodiversity and productivity, including the effects of stressors. He uses this information to deduce strategies for conservation and restoration.

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