

Assessing climatic and spatial variables influencing zooplankton richness for space-for-time predictions

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Abstract

1. The macroecological drivers of freshwater diversity are accredited geographical, spatial and climatic variables, but also to productivity, ecosystem age and landscape history. Locally diversity is also influenced by the dispersal ability of species. Here we evaluated how spatial and climatic variables influence species richness and macroecological patterns in Cladocera and Copepoda. We also discuss whether a space-for-time approach is suitable to predict the community's response to the current rapid warming of lakes.
2. We use the presence-absence of pelagic and littoral microcrustaceans in 1465 Norwegian lakes with a wide range of latitudinal, longitudinal, and altitudinal gradients, as well as a wide span in lake areas, to evaluate how spatial and climatic factors influence zooplankton diversity in two major groups: Cladocera and Copepoda.
3. Longitude and latitude *per se* were poor predictors of zooplankton richness, but a combination of spatial and ecological predictors gave a good spatial prediction of cladoceran and copepod richness. These two groups did, however, not differ in their spatial distribution, with a strikingly fixed proportion of copepods close to 0.3, suggesting no obvious Allee- effects regarding the mode of reproduction (asexual vs sexual).
4. Since temperature alone was a poor predictor of species richness for both groups and dispersal constraints can make it very difficult to estimate a new richness equilibrium under a future climate, space-for-time predictions may have limited value for assessing future patterns of microcrustacean diversity.
5. Based on a quite unique dataset in terms of the sheer number of sites, spatial gradients, and inclusion of littoral species, our study demonstrates that assessments on how changing climate will shape and modulate zooplankton communities in the future are problematic.

KEYWORDS

biogeography, dispersal, diversity, lakes, micro-crustaceans

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1 | INTRODUCTION

A range of factors determines the spatial distributions of species, community composition and species richness, from apparently stochastic events to well-established drivers such as temperature, productivity or niche differentiation. Many studies covering a wide variety of ecosystems and organisms demonstrate that species richness tends to vary strongly with ecosystem area and productivity and habitat heterogeneity (Rosenzweig, 1995). However, as heterogeneity also can co-vary with habitat area or productivity (Honkanen et al., 2010; Lewis & Nocera, 2006), the role of niche diversity *per se* may not be separated easily from other causal factors.

Most taxonomical groups show decreased diversity with latitude and altitude (Gaston, 2000). This also applies to freshwater zooplankton (Hessen et al., 2006, 2007; Shurin et al., 2007), although species richness is less correlated with latitude in freshwater animals compared to terrestrial and marine species (Hillebrand, 2004). Compared to other habitats, lake ecosystems have the advantage of well-defined boundaries that define a single natural scale for studying their biodiversity, especially if the size range of investigated lakes is constrained (cf. Dodson, 1992). However, also for lakes, community composition and richness within any given locality are influenced by the likelihood of local dispersal.

The macroecological drivers of freshwater diversity include temperature, growing season length, productivity and covariates of these, but also ecosystem age and landscape history. There is, however, striking difference in the macroecology of different freshwater taxa, where some adhere to the classical latitudinal declines typically found for most terrestrial and marine organisms, while others do not (Heino, 2011). Immigration constraints could be part of the explanation for this, which again is related to geographical barriers, dispersal and colonisation (and Allee-effects), as well as local sorting (Andersen et al., 2020; Henriques-Silva et al., 2016). Also, macroecological patterns may differ with scale, where latitudinal gradients may be observed in regional studies but absent in global studies (Heino, 2011).

There is a general gradient in immigration history for both plant and animal species from east to west since the last glaciation of northern Europe 10,000 years ago, which partly explains the pronounced congruence in diversity across trophic levels (phytoplankton, zooplankton and fish) with strikingly lower diversity for all groups in western lakes (Andersen et al., 2020).

Lakes worldwide experience rapid warming (O'Reilly et al., 2015), affecting aquatic species' thermal niches (Kraemer et al., 2021). To the extent that patterns in biodiversity can be attributed to temperature or associated variables such as growing season, it can, in principle, be used to predict community responses by a space-for-time approach (Blois et al., 2013). For example, under a temperature change corresponding to a given number of degrees northward displacement or altitudinal shift (Montgomery, 2006), one would assume that a new equilibrium of community composition would establish at the expense of cold-adapted species (Lindholm et al., 2012) but in general, causing increased diversity (Hessen et al., 2007).

There will no doubt be a major time lag for “new” communities or diversity equilibria to establish, depending on the dispersal and colonisation ability of zooplankton, as well as ecosystem connectivity and beta diversity. Space-for-time assessments also depend on the extent to which climate and temperature are the key determinants of communities and diversity.

Technically, the littoral free-swimming micro-crustaceans are not true zooplankton, but there is a substantial overlap in species between pelagic and littoral samples. They are often collectively labelled zooplankton for convenience, rather than micro-crustaceans. Cladocera and Copepoda, which are the two major groups, cover the same size range and serve similar functional roles in pelagic food webs by linking primary production to secondary consumers such as fish. However, the groups differ in basic morphological features and life-cycle strategies. A major trait difference is that while copepods reproduce exclusively sexually, cladocerans reproduce mainly asexually through cyclical, or in cases also obligate, parthenogenesis. Copepods also typically have several developmental stages, first naupliar, then copepodite stages before maturation, whereas cladocerans have direct development and go through several moults before maturation. Different life cycles, notably sexual mode, can influence the dispersal ability since, in a parthenogenetic animal, a single individual may be sufficient to establish a new population, making it more likely to happen than for a sexually reproducing species. However, once established, sexual species are thought to be more adaptable to new conditions owing to reduced fixation of deleterious mutations (McDonald et al., 2016), producing new and potentially favourable genetic associations to deal with changing conditions (Bürger, 1999), and a better ability to cope with parasites (Hamilton & Axelrod, 1990). However, it does not necessarily always need to lead to adaptive genetic variability in the offspring, which can reduce the advantage of sexual reproduction under stable conditions (Otto & Lenormand, 2002).

Here we use the presence-absence of zooplankton in a large Norwegian dataset (1,465 lakes) spanning a wide range of latitudinal, longitudinal and altitudinal gradients, as well as a wide span in lake area, to evaluate potential spatial and climatic factors influencing species richness and macroecological patterns in Cladocera and Copepoda. These data are unique not only in terms of the sheer number of sites, but also in that all sites include littoral samples that hold the majority of zooplankton species (Walseng et al., 2006). The comparison between Cladocera and Copepoda also is interesting because of their different modes of reproduction, with cladocerans generally being facultative parthenogens and copepods reproducing strictly sexually. Asexual reproduction would *a priori* imply fewer constraints by Allee-effects, and thus higher colonisation abilities.

Finally, we discuss the potential for using linkages between climate and spatial patterns of diversity to make space-for-time predictions of zooplankton richness and community composition in the future. If so, what would this “future” imply? Is it possible to provide a meaningful timeline for establishing new equilibrium communities and diversity based on given climate scenarios?

2 | METHODS

2.1 | Data source and treatment

We used the presence and absence data of zooplanktons (Cladocera and Copepoda) from 1,465 Norwegian lakes where both pelagic and littoral samples were taken. These lakes cover a wide span in lake area, catchment properties, latitude, longitudes and altitudes, and hence also a wide range of temperatures. Lakes that have been surveyed for more years are represented by maximum 10 visits over 2 years, picked out randomly to reduce bias in species richness for these lakes. For total species number, littoral samples will encompass the vast majority of species (Walseng et al., 2006). For pelagic samples, vertical net hauls were taken during daytime from just above the bottom to the surface, using a standard plankton net with 90- μ m mesh size and a diameter of 30 cm. The littoral species were sampled by a net haul (27.5–30 cm, 90 μ m) horizontally, both outside and inside vegetation whenever possible in each lake.

Samples were preserved with formalin or Lugol and kept cool and dark until analysis. All crustaceans except cyclopoid and calanoid nauplii were identified to species. Most cladoceran species were identified according to Flößner (2000), whereas most copepods were identified after Kiefer (1978). The taxonomic affinities are not finally settled for some taxa, for example *D. longispina*, where recent genetic screening of both mitochondrial and nuclear markers has revealed a need for revised systematics (Hobæk, 2005; Schwenk et al., 2004). Genetic screening to detect cryptic species was beyond the scope of this survey, but it is undoubtedly an interesting aspect in macroecological analysis, notably when comparing cladocerans and copepods. Cryptic diversity is well-documented in both groups (Kochanova et al., 2021), yet since annual recombination also takes place in cladocerans, it is not obvious that cryptic diversity between these groups differs.

The dataset lists 126 species, including 78 cladoceran and 48 copepod species. The dataset is available on figshare (see data availability statement). The spatial occurrence of all individual species is provided in Figures S1 (Cladocera) and S2 (copepods).

In order to avoid that differences in sampling effort and date affected the results, we first clustered the lakes using a *k*-means algorithm (Hartigan & Wong, 1979) based on longitude, latitude, and

altitude. We assigned the lakes to 300 clusters over the Norwegian mainland, and ensured that the majority of the clusters contained at least three lakes. To do so, we repeated the clustering process and testing whether the requirement was met or not. If the loop did not yield any solution after 300 repetitions, we used the last clustering run, but even in these cases, most clusters had three or more lakes (median number of lakes per cluster was 4 [mean 4.8, SD 3.2]). We then calculated the species richness for each cluster. This procedure also would reduce regional stochasticity caused by different connectivity among lakes.

Climate data downloaded from worldclim.org (Fick & Hijmans, 2017) was extracted for each lake coordinate (using a raster package; Hijmans, 2021), and then averaged over each cluster. From the climate variables, we chose a subset where we could not detect any (obvious) collinearity between selected variables and which, based on general knowledge of zooplankton ecology and previous studies (Hessen et al., 2006), would be likely to affect the distribution of zooplankton species. These were the mean temperature of the warmest quarter, the seasonality in precipitation (coefficient of variation in precipitation), and the annual temperature range (Table 1; Figure S3).

2.2 | Data analysis

In our analyses, we use the pure species richness as indicator for zooplankton diversity. To determine spatial and abiotic environmental factors potentially influencing zooplankton species richness, we used three different generalised additive models (GAMs) assuming Poisson-distributed data. Each model had the species richness of the respective group as the dependent variable. The first model only used spatial information in the form of longitude and latitude (SPA), the second used climatic variables and lake size (ENV), and the third included all factors (SPAENV). We also added lake size and its interaction with the temperature of the warmest quarter in the ENV model, as we hypothesised that small lakes might be more affected by higher temperatures. These models were applied to each species of copepods and cladocerans separately.

We chose GAMs to allow for nonlinear responses. Latitude and longitude were implemented together as tensor product smooths. We

TABLE 1 Definition and summary statistics of the Bioclim variables, as well as the variable Lake area that was included as modelling terms in the analysis.

Bioclim code	Variable	Definition	Average (SD)	Min	Max
BIO10	Mean temperature of the warmest quarter (°C)	Mean temperature of warmest quarter (°C)	11.38 (2.57)	5.00	16.20
BIO15	Seasonality in precipitation	Coefficient of variation of yearly precipitation	27.32 (4.04)	17.00	48.00
BIO7	Annual temperature range	Interval from minimum to maximum temperature (°C)	24.68 (4.13)	15.10	38.80
	Lake area (ha)	Surface area of the lake (ha), log-transformed before analysis	2.29 (12.76)	0.00001	300.000

included the interaction between lake area and the mean temperature of the warmest quarter as tensor product interaction, together with single smooth terms for both factors, to be able to estimate also the contribution of the single effects. We used restricted maximum likelihood for parameter estimation of the models and allowed the fitting procedure to penalise and remove terms entirely from the model “mgcv” package (Marra & Wood, 2011) within R (R Core Team, 2022). As some lakes were visited more than once, we accounted for the different number of visits (averaged by cluster) by adding normalised weights (Visits/mean [Visits]) to the model formulation.

In order to test the predictive power of the model and choose the best model, we further randomly divided the clustered dataset into a training (70%) and validation dataset (30%). We choose the model with the highest explained deviance as the best model. The best model was then applied to the validation dataset to determine the explained variance R^2 (see Table 2) via a simple linear regression between predicted and actual species richness.

In order to estimate how much of the variance could be solely explained by the spatial or environmental variables, we also performed a deviance analysis. The proportion of variation explained by spatial terms was calculated by $\text{Prop}_{\text{SPA}} = (\text{deviance}_{\text{ENV}} - \text{deviance}_{\text{SPAENV}}) / \text{deviance}_{\text{Nullmodel}}$, the proportion explained by environmental terms using $\text{Prop}_{\text{ENV}} = (\text{deviance}_{\text{SPA}} - \text{deviance}_{\text{SPAENV}}) /$

$\text{deviance}_{\text{Nullmodel}}$, and the proportion explained by both factors using $\text{Prop}_{\text{SPAENV}} = \text{deviance}_{\text{SPAENV}} / \text{deviance}_{\text{Nullmodel}}$.

In order to ensure that the results were sensitive to the clustering algorithm, we ran the complete analysis including the clustering 1,000 times. The model predictions and coefficients (Table 2) were estimated using the full model (SPAENV) on the training dataset, and represent the average (\pm SD) of all simulations.

In order to visualise the effect of single model terms, we used the average value for each of the other factors of the models (Figure 1). We then used the full data range of the respective variable to predict the response in species richness. To test how the full models estimated by the training dataset would be able to predict the conditions of single lakes, we used the original lake dataset with its corresponding bioclimatic variables to predict and map the species richness and its prediction error in different lakes (Figure 2).

2.3 | Proportion of copepod species

The mode of reproduction and other inherent ecological differences between copepods and cladocerans could impact dispersal likelihood. Hence, for example, Allee-effects could favour asexual Cladocera in marginal areas (Henriques-Silva et al., 2013, 2016). To

TABLE 2 Averaged model coefficients of the full model (SPAENV) from 1000 model runs.

	Edf, mean (SD)	χ^2 , mean (SD)	p-value, mean (SD)	R ² (%)
Copepoda				
te(latitude, longitude)	7.47 (3)	45.61 (28.87)	0.004 (0.03)	55
ti(Area, BIO10)	2.37 (1.66)	12.24 (9.28)	0.048 (0.136)	
s(BIO10)	2.48 (0.96)	68.65 (32.29)	<0.001 (<0.001)	
s(Area)	3.69 (2.24)	46.71 (18.02)	<0.001 (<0.001)	
s(BIO15)	0.73 (0.83)	2.41 (3.37)	0.293 (0.293)	
s(BIO7)	1.12 (1.15)	6.5 (9.46)	0.206 (0.276)	
Cladocera				
te(latitude, longitude)	6.94 (3.54)	44.5 (33.18)	0.03 (0.113)	62.6
ti(Area, BIO10)	4.98 (2.54)	23.01 (13.93)	0.024 (0.093)	
s(BIO10)	2.01 (1.21)	175.64 (98.17)	<0.001 (<0.001)	
s(Area)	5 (2.77)	63.05 (24.02)	<0.001 (<0.001)	
s(BIO15)	0.66 (0.91)	2.7 (4.5)	0.316 (0.309)	
s(BIO7)	1.32 (1.48)	9.28 (13.82)	0.218 (0.287)	
Proportion of copepods				
te(latitude, longitude)	0.65 (0.51)	1.56 (1.65)	0.258 (0.251)	8.6
ti(Area, BIO10)	0.28 (0.7)	0.92 (2.97)	0.527 (0.311)	
s(BIO10)	1.23 (0.79)	3.67 (3)	0.168 (0.194)	
s(Area)	0.11 (0.38)	0.32 (1.64)	0.606 (0.267)	
s(BIO15)	0.10 (0.24)	0.21 (0.58)	0.562 (0.256)	
s(BIO7)	0.43 (0.33)	1.05 (1.09)	0.21 (0.171)	

Note: Standard deviation (SD) is reported to assess the sensitivity of the model results to the clustering procedure. Estimated degrees of freedom (edf) around 1 indicates a linear relationship, higher values a nonlinear relationship, while values approaching 0 indicate no relationship. BIO10 corresponds to the mean temperature of the warmest quarter, BIO15 to the seasonality in precipitation, BIO7 to the annual temperature range. See Table 1 for more details.

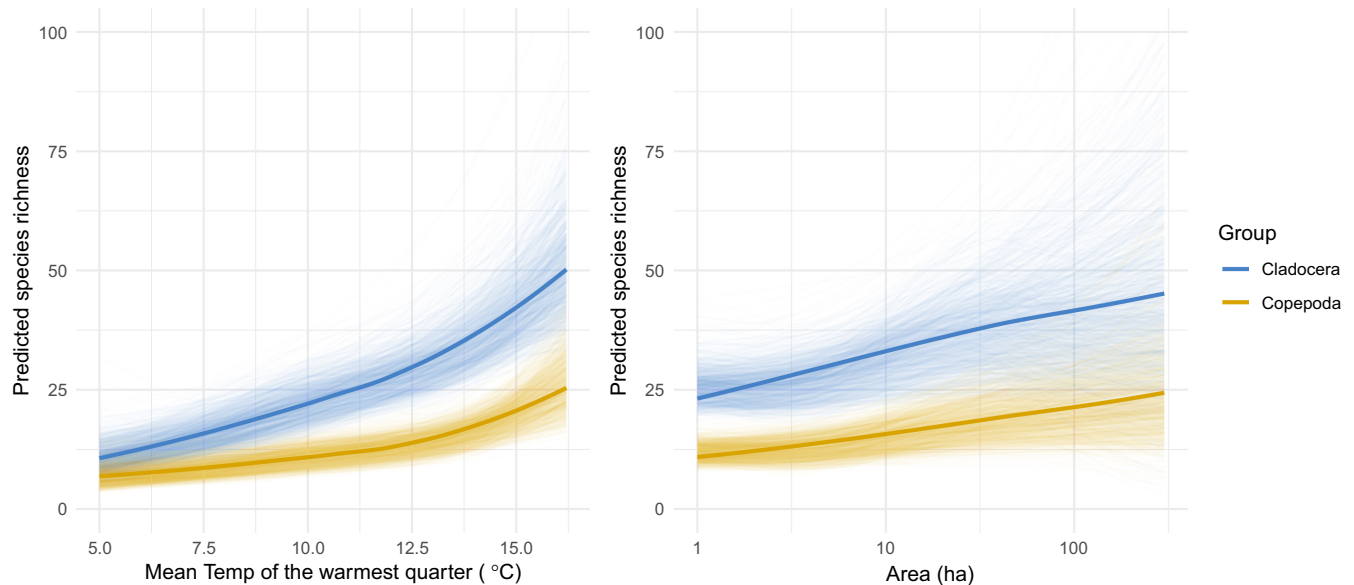


FIGURE 1 Model predictions for Copepoda and Cladocera species richness for the mean temperature of the warmest quarter and lake area; absent model parameters in each plot are set to the average value. Faint lines represent individual predictions of each of the 1,000 models, whereas the dark line gives the smoothed (loess) average over all simulations.

test which of the same environmental and spatial factors affected the ratio of copepods to the total number of species, we also formulated a GAM with a binomial distribution. As before, we formulated all three model types with their respective terms: spatial (SPA), climatic + lake size (ENV), and full model (SPAENV); and repeated the entire analysis, including the clustering, 1,000 times.

3 | RESULTS

For both Cladocera and Copepoda, longitude, latitude, summer temperature and lake area influence the species richness (Figure 1; Table 2). There was a positive relationship between species richness and both average summer temperature (Figure 1a) and lake area (Figure 1b). The interaction between summer temperature and lake area showed a generally weak positive effect on species diversity in larger lakes (Table 2; Figures S4A and S5A). Effects of annual temperature range and seasonality in precipitation also were not conclusively supported by the model (Table 2; Figures S4B,C and S5B,C).

For both taxa, species richness decreased with latitude and from east to west, especially in Southern Norway (Figure 2). When tested against the original lakes, the models seemed to capture species-richness patterns in Norway well (Figure 2e,f). However, it is apparent that the models seemed to overestimate the number of species in both groups, especially in the southeast of Norway.

Variance partitioning yielded similar results in Copepoda and Cladocera (Figure 3). For copepods, longitude and latitude alone explained on average 11.7% (*SD* 9.4) of the variance in species richness, whereas the environmental variables alone explained 24.1% (*SD* 6.2); 68.4% (*SD* 3.6) was explained by a combination of both factors. On

average 32.7% (*SD* 11.5) of variation could not be clearly assigned to either of these factors, and interaction of these factors influenced the dependent factor. In cladocerans, the variance partitioning analysis revealed that on average longitude and latitude alone explained 8.3% (*SD* 8.1) of the variance in species richness, whereas ecological variables alone explained 30.3% (*SD* 11.9); 73.1% (*SD* 3.4) of the variation was explained by a combination of both factors, which means that on average, 34.5% (*SD* 15.6) of the variation could not be clearly assigned to either of these factors.

3.1 | Proportion of copepods in the lakes

When analysing the relative contribution of the copepods and cladocerans to lake biodiversity, we found that none of the considered factors influenced the proportion of copepods in the lakes (Figure S6; Table 2). On average, the models only explained 8.6% of the variance. The proportion of copepods in the model clusters was strikingly constant at 0.31 (*SD* 0.071) between model runs, but it is important to state that this does not imply that all individual lakes possess this ratio.

Behind these aggregated data on richness is of course a strong variability at the species level. Some were apparently jack-of-all-trades, with a widespread distribution across most waterbodies, the extreme being the cladoceran *Bosmina longispina*, which occurred in >80% of all locations, whereas others were confined either to specific waterbodies or specific regions. An evaluation of these patterns and strategies at the species level is beyond the scope of this work, but the spatial occurrence of all individual species is provided in Figures S1 (Cladocera) and S2 (Copepoda).

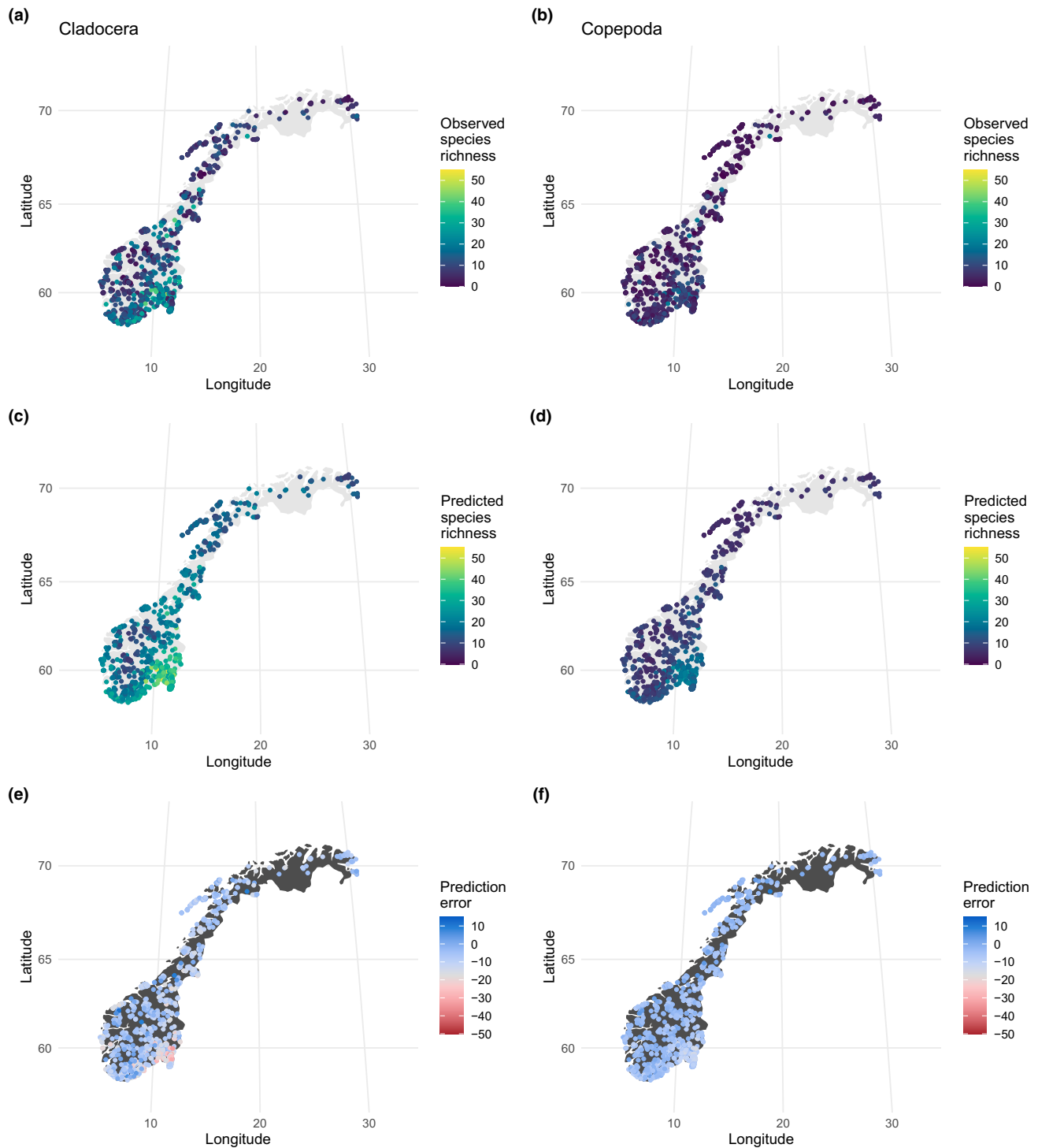


FIGURE 2 Observed (a, b) and predicted (c, d) species richness in the sampled lakes and the average prediction error (e, f) of the models trained on clustered data when tested on the original lake data.

4 | DISCUSSION

The striking gradient in species richness declining with latitude and increasing with longitude, which results in a maximum in the southeast of Norway, confirms the expectation of macroecological patterns with higher richness at high temperatures. Still, the statistical predictions based on temperature alone are very

modest, partly related to confounding factors along the gradient such as productivity and post-glacial immigration (Hessen et al., 2006). This also reflects a high impact by local, unexplained or even stochastic factors (cf. Andersen et al., 2020), although we believe that our method assigning all lakes to 300 clusters, has made our data robust and compensated for differences in sampling effort.

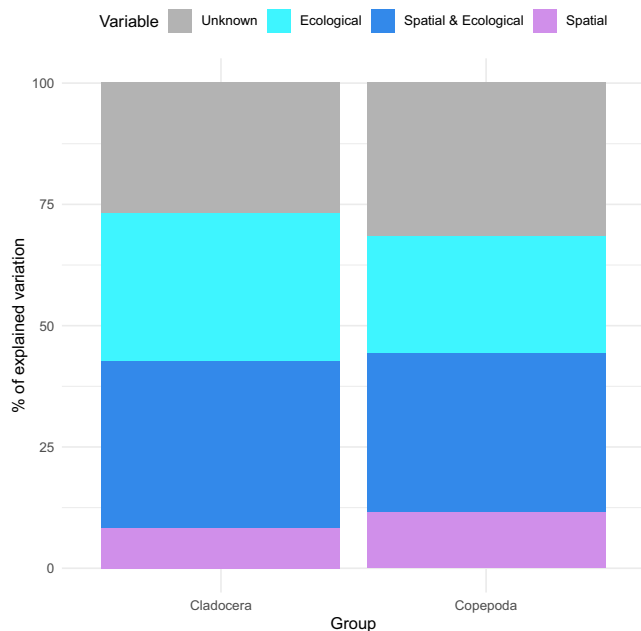


FIGURE 3 Results of the variance partitioning analysis for Cladocera and Copepoda showing the relative contributions of spatial and ecological variables in explaining the variation in species richness. The blue areas indicate variation that could not clearly be assigned to one or the other explanatory variables.

The output from the GAM supports the two major macroecological theories for spatial richness; Wright's (1983) species-energy theory and Rosenzweig's (1995) species-area theory. Energy input can both be direct solar energy converted to temperature and organic energy from primary production (Hessen et al., 2007), and these are spatially correlated in these northern lakes. The two theories are not mutually exclusive; in fact, they are likely to be additive, but judging from Figure 1, the energy (temperature) is the more important and likely to reflect the wide climatic gradient. Moreover, in the context of space-for-time predictions, energy or productivity is the relevant variable, whereas area clearly is not.

Longitude and latitude were poor predictors of diversity compared to climatic and ambient factors for both copepod and cladocerans. Models with both factor groups included explained much more variation than the additive contributions of spatial and ecological models. This indicates that there must be small-scale interactions between these factors that perform a locality-specific species sorting. The number of established species also might be influenced by the length of the colonisation period, monopolisation effects (De Meester et al., 2016) and other factors.

More than 30% of the observed variance was left unexplained for both groups, supporting the findings of Andersen et al. (2020) in a much smaller dataset, yet sampled in a synoptic survey along an east-west gradient with minor climatic differences in summer. Model performance was especially poor in the species-rich south-eastern region.

Cladocerans had consistently higher diversity than the copepods, yet we could not detect any macroecological differences between

the two. Some studies have suggested an Allee-effect favouring the asexual cladocerans in marginal or species-poor habitats (e.g., Henriques-Silva et al., 2013, 2016; Pinel-Alloul et al., 2013), yet we found no evidence for this in our extensive dataset that also covers a very extensive gradient of lakes in terms of latitude and altitude, as well as temperature and productivity. This could reflect differences in topography and geography as well as glaciation history and glacial refugia between Scandinavia and North America, but also that Allee-effects might be less prevalent than expected—that is, mate limitation only seems to occur at very low population densities in copepods (Choi & Kimmerer, 2008; Williamson & Butler, 1987). However, since we have no information about population sizes, we cannot exclude Allee-effects. We also might have recorded a “survivor bias”, where repeated population crashes might have occurred over time, but by now, most of the possible range expansions have been achieved. It also is worth remembering that a unique feature of our data includes the littoral zooplankton that generally encompass more than two-thirds of species found in a lake (Walseng et al., 2006). The proportion of copepods is remarkably stable at around 0.31 (SD 0.08) in lakes of all regions and also in the typically cyprinid-dominated south-eastern lakes (Hessen et al., 2006). Yet, the communities *per se* differ regionally and typically with smaller zooplankton species in the cyprinid-dominated systems (Hessen et al., 1995). Our findings support Cohen and Shurin (2003), who found no consistent dispersal differences between these groups. Instead, species of both cladocerans and copepods ranged from highly effective to slow dispersers.

Apart from the most species-rich region, the spatial predictions were quite robust, meaning that spatial predictions indeed can be made for geographical patterns of richness. *A priori*, this also should allow for future prediction of richness (and even community composition) under future climate scenarios (i.e., space-for-time predictions). This has been demonstrated to work for plant communities judged from regional pollen analysis for different climates (Blois et al., 2013). Space-for-time predictions for zooplankton communities have some constraints, however. Firstly, spatial predictors or temperature performed poorly alone. Secondly, establishing a new spatial equilibrium of community composition in response to climate change depends on the zooplankton's dispersal and colonisation ability. The biogeographical distribution patterns of species depend on the ability of species to disperse to and establish in new ecosystems. For species scattered within a region, one would suspect that their absence or presence in nearby lakes can be attributed to lake-specific properties or random events (ecological drift *sensu* Vellend, 2010). Dispersal abilities may, however, be hard to separate from ecosystem properties, climatic patterns and landscape history for species with pronounced distributional patterns across geographical clines.

Dispersal constraints should presumably be less for cladocerans than copepods, but our dataset does not support it. Fish and birds may spread the resting stages of most cladocerans and a few copepods via gut survival (Banarescu, 1990; Green & Figuerola, 2005). Resting eggs (ephippia) may resist freezing and desiccation, and hatch after extended periods (Weider

et al., 1997). They may disperse by wind, water or by biological vectors, and their facultative asexual mode of reproduction and fast growth rates (classical properties of “r-selected” organisms) should *a priori* suggest superior dispersal abilities in cladocerans relative to most copepods. However, this may not always be the case (Cáceres & Soluk, 2002). And indeed, the proportion of copepods is quite constant in all analysed lakes. Among the copepods, different dispersal abilities also can be related to the resting stage strategies (Zeller et al., 2006), but might be more related to movement through water (Maly & Bayly, 1991).

Local zooplankton colonisation seems to occur within a decade (Arnott et al., 1998; Havel & Shurin, 2004; Shurin, 2000; Shurin et al., 2000). There is no consensus, however, on how much dispersal has been achieved by zooplankton at different regional scales (Bohonak & Jenkins, 2003). The general assumption of high dispersal abilities also is countered by studies on local genetic affinities that suggest rather limited gene flow at the meta-population scale (De Meester et al., 2002). On scales of tens to hundreds of kilometres, dispersal constraints are more likely (Havel & Shurin, 2004; Hessen et al., 2019). This could explain why, in this dataset, southern and eastern immigrants were poorly represented in the richness measures of the northern and western lakes.

The assumption of ongoing post-glacial colonisation is shared by studies on terrestrial wind dispersers, particularly trees. Several tree species of northern Europe dispersed from northeastern glacial refugia at slower rates than assumed previously (Feurdean et al., 2013). The estimated dispersal velocity of spruce is less than 100 m/year, which is consistent with its natural absence from the west coast of Norway. The striking decline in zooplankton diversity along an east-to-west gradient in Scandinavia, cannot be attributed to temperature differences, suggesting colonisation constraints since the termination of the last glaciation (Andersen et al., 2020; Hessen et al., 2006). The mountains separating western Norway from central Norway and Sweden may act as a dispersal barrier. When we look at the species-specific occurrences, we see that several species were recorded only in the east of the mountain ridge.

Productivity and fish predation also will impact community composition. Yet data for nutrients and phytoplankton, or fish community composition or biomass were only available for a very limited number of lakes and, hence, not included in our analysis. Nevertheless, previous studies on different (and much smaller) datasets of Norwegian lakes have not provided evidence for strong impacts of productivity and fish for biodiversity *per se*, but it is difficult to separate the impact of productivity and fish from spatial covariates owing to the strong covariation of these factors (Andersen et al., 2020; Hessen et al., 2006, 2007).

In order to further resolve the influence of spatial and environmental factors, one would need quantitative abundance data for the different species. To be comparable, one would need to be able to correct for the season, time of day and other environmental factors. While this can be achieved at smaller scales (see, e.g., Kruk

et al., 2022), it is difficult at the macroecological scales of this study, and macroecological patterns may differ between local, regional or global studies (Heino, 2011). Moreover, it is inherently more difficult to get precise abundance data for littoral species than for pelagic species.

To summarise, based on a truly extensive dataset, we have demonstrated that longitude and latitude *per se* are poor predictors of zooplankton richness, but that a combination of spatial and ecological predictors actually worked well in predicting copepod and cladoceran richness. These two groups did, however, not differ in their spatial distribution with a strikingly fixed copepod proportion close to 0.31, suggesting no obvious advantage of asexual reproduction across spatial scales. This does not mean that all lakes possess this ratio. The clustering approach might somewhat contribute to stabilising the relative proportions of cladocerans and copepods. The dominance of cladocerans stands firm, however, and we can only speculate on the causality of this ratio between the two major groups of micro-crustaceans, and while reproductive mode could be one, so could be their evolutionary origin. Cladocera are considered a monophyletic group with freshwater origin (Van Damme & Kotov, 2016), whereas marine copepods have repeatedly colonised freshwater habitats (Boxshall & Jaume, 2000). Moreover, their feeding mode or other functional traits could play a role for the prevailing cladoceran dominance both in littoral and pelagic habitats. Most cladocerans are non-selective filter-feeders and together may efficiently monopolise a broad range of food items (Hessen, 1985). Since temperature alone was a poor predictor of richness for both groups and because dispersal constraints make it very difficult to estimate a new richness equilibrium under a future climate, space-for-time predictions may have limited value for the assessment of future patterns of zooplankton diversity.

AUTHOR CONTRIBUTIONS

Conceptualisation: Dag O. Hessen, Tom Andersen, Jan Heuschele, Bjørn Walseng. *Developing methods:* Bjørn Walseng, Dag O. Hessen, Jan Heuschele, Tom Andersen. *Data analysis:* Jan Heuschele, Tom Andersen, Dag O. Hessen. *Preparation of figures and tables:* Jan Heuschele. *Conducting the research:* Bjørn Walseng, Jan Heuschele. *Data interpretation, writing:* Dag O. Hessen, Jan Heuschele, Tom Andersen, Bjørn Walseng.

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CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data can be downloaded from Figshare (<https://figshare.com/s/c56c35bbc7472f287ad5>). The zip file also includes the code used to run the analysis.

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SUPPORTING INFORMATION

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