

Research

Climate change impacts on body size and food web structure on mountain ecosystems

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The current distribution of climatic conditions will be rearranged on the globe. To survive, species will have to keep pace with climates as they move. Mountains are among the most affected regions owing to both climate and land-use change. Here, we explore the effects of climate change in the vertebrate food web of the Pyrenees. We investigate elevation range expansions between two time-periods illustrative of warming conditions, to assess: (i) the taxonomic composition of range expanders; (ii) changes in food web properties such as the distribution of links per species and community size-structure; and (iii) what are the specific traits of range expanders that set them apart from the other species in the community—in particular, body mass, diet generalism, vulnerability and trophic position within the food web. We found an upward expansion of species at all elevations, which was not even for all taxonomic groups and trophic positions. At low and intermediate elevations, predator:prey mass ratios were significantly reduced. Expanders were larger, had fewer predators and were, in general, more specialists. Our study shows that elevation range expansions as climate warms have important and predictable impacts on the structure and size distribution of food webs across space.

Keywords: emergent ecosystems; ecological networks; vertebrates; alpine environment; climate warming; body size

1. INTRODUCTION

Climate change is expected to be the major threat to biodiversity and one of the main factors affecting human health and well-being in the coming decades [1]. The current distribution of climatic conditions will be rearranged across the globe over the present century [2]. Living organisms must adapt to novel and rapidly changing conditions, and so species must keep pace with climates to survive. Because of differences among species in tracking optimal environmental conditions, climate change will probably have profound effects on community organization and dynamics, as well as on ecosystem functioning [3,4].

Mountain ecosystems occur on all continents, in all latitudinal zones and within the entire world's main biome types. They support a large portion of the world's biological diversity [5,6], and are among the most affected and threatened as a result of climate change and population movements [7,8]. Mountain species with narrow habitat tolerances and/or low dispersal ability are at high risk in the face of climate change [9].

Recent climate change [10] has already impacted biological systems worldwide [11–13] and has led to

significant shifts in the distribution, phenology and behaviour of species [11,14,15]. In parallel to latitudinal movements, species inhabiting mountain regions are expected to move upwards to higher, cooler elevations as temperatures rise. Upward movement of alpine plants has already been documented [16], with changes in community composition at high elevations [17]. A median shift of 11.0 m uphill per decade for several plant and animal species has been detected [15,18].

Different temporal and/or spatial responses of different taxonomic groups can lead to mismatches between interacting species. Spatial mismatches will take place when interacting species shift their ranges at different speeds [3,4,15,19–24]. Broken and novel interactions resulting from spatial mismatches will probably alter species abundances, distributions and extinction probabilities of species under climate change. However, the question of how climate change will modify community structure and dynamics is still far from being solved [3,4]. A major challenge is to predict which species will more likely expand their ranges, whether range expanders have particular traits and the consequences of differential range expansions on the structure and dynamics of the food web within which these species are embedded. Because of its fundamental relation to animal metabolism and its role on community organization and food web structure [25–28], body size can be one of these traits [29]. Other traits that might explain the success of expanding species are linked to their position within the food web [30].

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One contribution of 17 to a Theme Issue 'Climate change in size-structured ecosystems'.

In this paper, we explore the effects of climate change in the highly diverse vertebrate food web of the south-eastern Pyrenees mountain range. By characterizing the occurrence of elevation range expansions of vertebrate species between two time periods that illustrate climate change, we investigate: (i) the changes in food web properties such as the distribution of links per species, community size-structure and the distribution of predator : prey body mass ratios; (ii) the taxonomic composition of range expanders; and (iii) some characteristics of expanders: body mass, diet breadth, vulnerability and trophic position. We do this using data compiled from the literature on habitats, distributions and trophic interactions among species in the Pyrenees.

2. MATERIAL AND METHODS

We have constructed food webs among vertebrate species combining a unique dataset of species distributions over the southeastern side of the Pyrenees mountain range with observations of their feeding links. The dataset comprises annual presence/absence information of vertebrate species on a geo-spatially located grid, including information on elevation and habitat types observed in each cell of the grid.

The study area includes the southeastern slopes of the Pyrenees (Iberian Peninsula side), from the highest creeks in the centre of the mountain range to the Mediterranean Sea in the east, covering a region of 900 000 ha with elevations between 255 and 3140 m.a.s.l. A climatic dataset was obtained by modelling climatic surfaces from discrete climatic data from the Spanish weather-monitoring system [31–33]. Climatic variables included temperature (°C), precipitation (mm) and the annual and summer precipitation to potential evapotranspiration (PPET) ratio [34]. For the purposes of this paper, annual data were aggregated for the elevation ranges considered (see below and electronic supplementary material, S1).

Food webs were constructed from existing databases and extensive bibliography search (see electronic supplementary material, S1 for detailed information about the food web construction). Spatial co-occurrence of species, and hence realized trophic links, were dependent upon three factors: (i) presence in the same grid cell, (ii) elevation and (iii) habitat coincidence. If a pair of species coincided in these criteria and the literature reported a trophic relationship among them, then a link was added to the food web between them. The whole elevation range was divided into three equally distributed elevations: low (from 255 to 1217 m), intermediate (from 1218 to 2179 m) and high elevation (from 2180 to 3140 m). One network for each elevation for each year over the period considered was constructed, resulting in a total of 54 food webs (18 for each elevation). The complete database comprised 253 species (13 mammal carnivores, 40 other mammals, 33 birds of prey, 133 other birds, 10 amphibians, 21 reptiles and three fish species). Temporal variability was studied by comparing two periods, referenced as pre (P1) and post (P2). P1 includes years between 1984 and 1990, both inclusive, and P2 comprises the period between 1991 and 2001 (see the

electronic supplementary material, S4 for an example of built food webs).

We examined the cumulative standardized degree distribution of the networks $P(k > K)$, which describes the fraction of species with a number of links k greater than K , for the P1 and P2 periods at each elevation [35]. Two different cumulative distributions were considered, that of the interactions of species with their predators (standardized outdegree), and the one representing their interactions with their prey or diet breadth (standardized indegree). Two other food web properties were analysed: the standard deviation of generalism (GenSD) and the standard deviation of vulnerability (VulSD).

We compared body mass distribution of newly arrived species over P2 at each elevation range with the body mass distribution of native species at that elevation to assess whether the species expanding their range upwards were larger than the natives. Analyses were carried out for all species together, by taxa (e.g. separating birds and mammals), by separating predator from prey species and by lumping species within trophic levels.

We also calculated the predator–prey mass ratios (PPMR) for all the links present in each web. This value, for each link, was calculated as the base-10 logarithm of the fraction between the body mass of the predator and the body mass of the prey. This allowed for the description of the distribution of these values in each web, and the statistical comparison of these distributions between the P1 and P2 periods.

Statistical analyses included generalized (GLM), mixed and general linear (LM) models, and Student and Kolmogorov–Smirnov tests. All analyses were carried out using R [36,37].

3. RESULTS

(a) *Climate*

Mean annual temperature increased during the whole period in the three elevation ranges. On average, mean temperature during P1 was significantly lower than during P2 at low and intermediate elevations (see the electronic supplementary material, figure S6), whereas at high elevations, these differences were not significant, although showing the same tendency (table 1). On the other hand, neither annual PPET nor summer PPET showed significant differences between P1 and P2 in any of the elevations (see the electronic supplementary material, figure S6).

(b) *Changes in food web properties*

(i) *Species richness*

Low and intermediate elevations showed similar and significantly higher number of species than high elevations (LM, $p < 2.2 \times 10^{-16}$). At the three elevation ranges, species richness was significantly higher in P2 than in P1 (table 1 and figure 1a–c). The number of new species (i.e. those present in P2 but not present in P1) was fairly constant across the entire elevation range (table 2). However, at high elevations, they represented a much larger proportion of the natives ($\chi^2 = 17.056$, d.f. = 2, $p = 0.000019$). Concerning the taxonomical composition of new species, most of them were birds, and within birds, most corresponded to basal species in

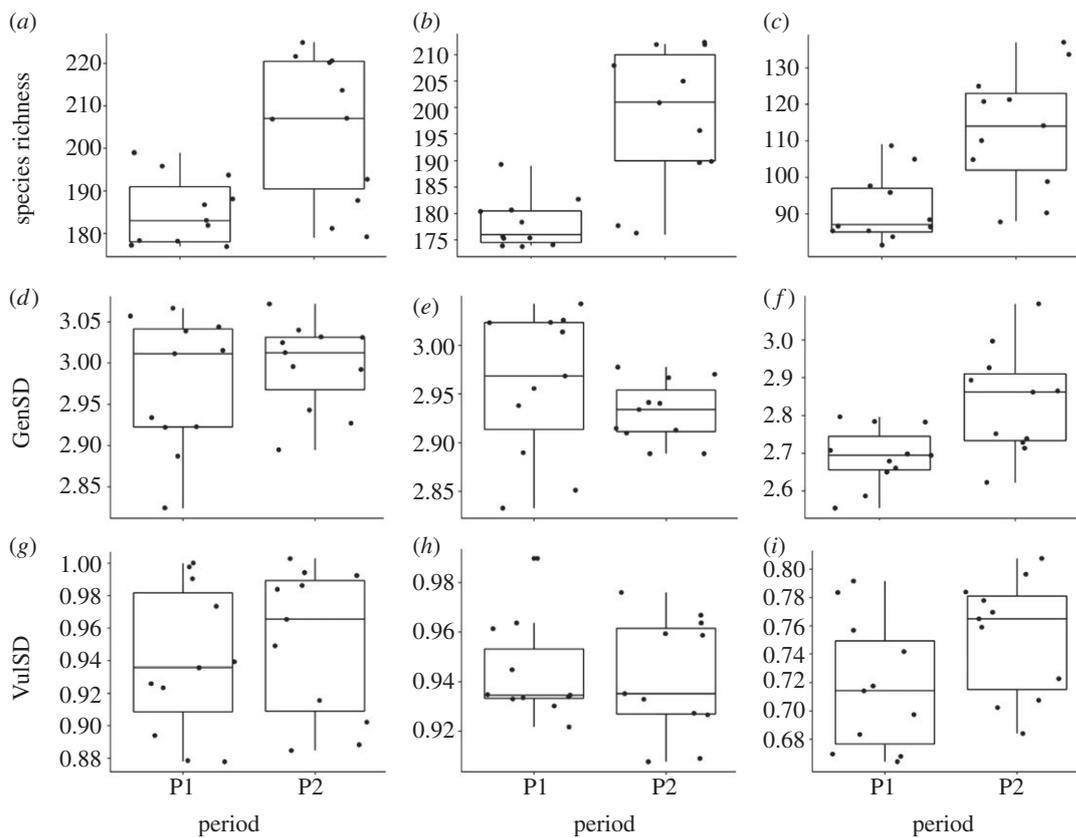


Figure 1. Mean values of food web properties at (a,d,g) low, (b,e,h) intermediate and (c,f,i) high elevations during P1 (1984–1990) and P2 (1991–2001) ((a–c) Species richness; (d–f) GenSD; (g–i) VulSD).

Table 1. Comparison of mean annual temperature ($^{\circ}\text{C}$), species richness (N), standard deviation of generalism (GenSD) and standard deviation of vulnerability (VulSD), between P1 and P2. Significant differences are marked in bold.

	elevation	P1	P2	d.f.: t	p -value
temperature	low	10.1	10.6	38.8: -3.29	0.002
	intermediate	7.1	7.6	37.5: -2.52	0.016
	high	3.2	3.6	34.6: -1.54	0.133
species richness	low	186	203	15.7: -2.88	0.011
	intermediate	178	197	14.3: -4.25	0.001
	high	92	111	17.6: -3.22	0.005
GenSD	low	2.98	2.99	14.9: -0.41	0.680
	intermediate	2.96	2.93	11.3: 1.04	0.320
	high	2.68	2.83	17.6: -3.39	0.003
VulSD	low	0.95	0.95	19.9: 0.02	0.980
	intermediate	0.94	0.94	19.8: 0.34	0.730
	high	0.72	0.75	19.5: -1.18	0.250

the food web. It should be noticed, though, that most top predators have large home ranges and are habitat generalists, and thus they were already present at all elevations in P1.

Most new species at each elevation came from lower elevations, indicating elevation range expansions (table 3). However, 23 per cent of the new species at low elevations seemed to have moved downwards, going from higher to lower elevations. Thus, 77 per cent and 64 per cent of new species at low and intermediate elevations, respectively, came from the surrounding areas, which, in the Pyrenees, correspond to lower elevations. This percentage was much lower at high elevations, where only 8 per cent of species had moved

from the surrounding lowland regions, whereas 92 per cent of the new species were already present at lower elevations within the Pyrenees, either low or intermediate, before 1990.

(ii) Diet generalism

Globally, the GenSD was significantly lower at high than at low and intermediate elevations (LM, $p < 0.0001$). GenSD significantly increased at high elevations from P1 to P2 (figure 1f), whereas differences between these two periods at the low and intermediate elevation ranges were not significant (table 1 and figure 1d–e).

Table 2. Distribution of new species (percentage) in period P2, according to the taxonomic classification used in this study within each of the three elevation ranges. Low elevation (255–1217 m), intermediate elevation (1218–2179 m), high elevation (2180–3140 m).

group	low elevation ($n = 41$)	intermediate elevation ($n = 40$)	high elevation ($n = 47$)
mammals	7.3	17.5	17
carnivores mammals	7.3	0	4.3
birds	68.3	55	53.2
birds of prey	14.6	20	14.9
reptiles	2.4	2.5	6.4
amphibians	0	5	4.3

Table 3. Percentage of new species at each elevation range and their origin between periods P1 and P2. ‘Surrounding’ corresponds to species coming from lower elevation surrounding areas. Low elevation (255–1217 m), intermediate elevation (1218–2179 m), high elevation (2180–3140 m).

origin	destination		
	low elevation	intermediate elevation	high elevation
surrounding	77	64	8
low elevation	—	33	48
intermediate elevation	16	—	44
high elevation	7	3	—

The distribution of the number of prey consumed by each predator (i.e. the standardized indegree distribution) during P1 and P2 was similar at all elevations (figure 2*a–c*). There was a common increase in specialist species, relative to the ones already present. There were slight differences between high elevations and the others, with steeper slopes in the former. However, in all cases, differences of the distributions between P1 and P2 were significant (Kolmogorov–Smirnov test, low elevation: $D = 0.37$, $p < 0.0001$; intermediate elevations: $D = 0.38$, $p < 0.0001$; high elevation: $D = 0.28$, $p = 0.0009$). This, united to the patterns of change observed above for GenSD, indicates that incoming consumer species at the high elevation range were more generalists—i.e. had broader diet breadths—than native consumers.

(iii) Vulnerability

The VulSD was significantly lower at high than at low and intermediate elevations (LM, $p < 0.0001$). VulSD did not change between P1 and P2 (figure 1*g–i*). This suggests that within an elevation range, predation pressure was equally distributed among prey species in the food web, and this did not change with changing climatic conditions and/or the arrival of new species.

Marked differences occurred, however, when comparing the number of predators attacking new and native prey between P1 and P2 (figure 2*d–f*). At all elevations, new prey species were exposed to fewer predators than their native counterparts ($D = 0.30$, $p < 0.0001$; $D = 0.35$, $p < 0.0001$; and $D = 0.38$, $p < 0.0001$, at low, intermediate and high elevations, respectively), as shown by steeper standardized outdegree distribution slopes for P2.

(c) Size-structure: predator–prey mass ratios

We compared the distribution of PPMR in the native food web (P1) with the distribution of mass ratios only

considering newcomers at P2 and their interaction with natives. At the three elevations, PPMRs at P1 were significantly higher, although only marginal at high elevations ($p < 0.0001$ at low and intermediate elevations, and $p = 0.06$ at high elevation) than at P2, indicating either an increase of big prey and/or a decrease of big predators from P1 to P2 (figure 3*a–c*).

The same result was obtained when only basal species and their predators were considered, with significant differences at high elevations as well ($p < 0.0001$, $p < 0.001$ and $p = 0.047$ at low, intermediate and high elevations, respectively). The analysis of the body mass of new species (see the electronic supplementary material, table S3) revealed that incoming basal species were generally larger, and thus the differences in PPMRs were likely due to an increase of big prey instead of a decrease of predator sizes.

(d) Expanders versus non-expanders: species traits

(i) Habitat generalism

Contrary to previous observations and expectations [38], expanders at intermediate and high elevations were not more habitat generalists than the natives at that elevation. A significant example is provided by incoming bird species at high elevations: they were more habitat specialists than native birds, occupying about half of the suitable habitats, regardless of their trophic level (see the electronic supplementary material, table S4).

(ii) Trophic relations

The mean standardized outdegree values of expanders were significantly lower than those of non-expanders, indicating that expanding species had few predators (both at the native and at the new elevation; table 1). On the other hand, we found no significant differences of the mean standardized indegree values between expanders and non-expanders for the whole period (table 1).

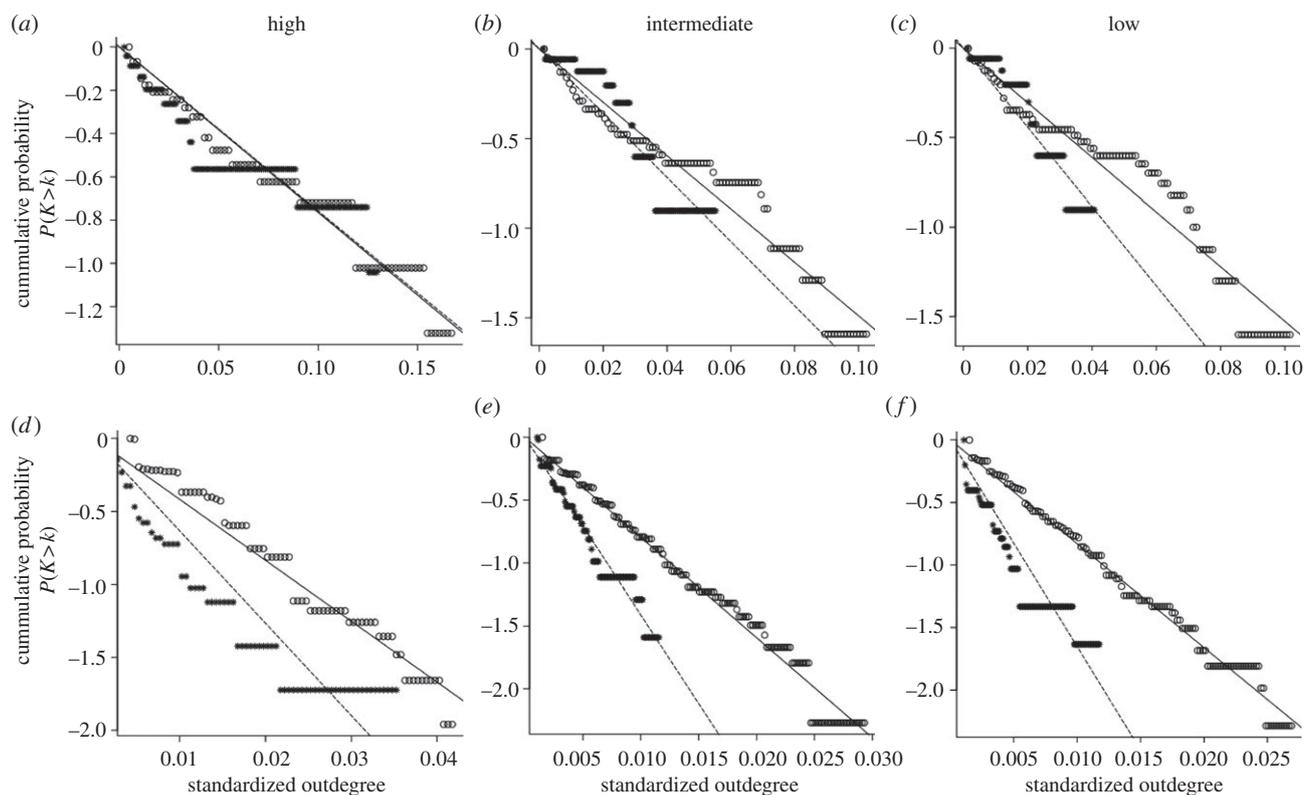


Figure 2. Cumulative probability distributions of the standardized indegree—number of prey species each predator feeds upon (a–c)—and the standardized outdegree—number of predators attacking each prey (d–f)—at each elevation range during the periods P1 (open circles, 1984–1990) and P2 (asterisks, 1990–2001).

(iii) *Body mass of expanders*

New prey species were significantly larger than natives at low and intermediate elevations ($p = 0.04$ and $p = 0.02$, respectively; figure 3d–e), whereas incoming prey at high elevations were not significantly larger than the natives (figure 3f). Observed differences at low and intermediate elevations were mostly due to range expanding birds, whereas differences in body mass between newcomers and natives were not observed for mammals and carnivores (see the electronic supplementary material, table S4). On the other hand, new predators at any elevation range were not larger than native predators, and hence predator body mass was not a good predictor of elevation range expansion in our data.

4. DISCUSSION

We show that mountain ecosystems are experiencing important changes in species composition, food web structure and community size distributions. Novel communities resulting from climate change are characterized by a higher proportion of larger basal prey species. We observed an upward expansion of species across the whole elevation range, with most expanders representing birds from low trophic positions. At low and intermediate elevations, new basal species were larger than native species, promoting significant changes in PPMR. At the highest elevations, new species were not larger than the natives, were more habitat specialists and, among the expanders, were the ones with more similar diet breadths than the natives. At all elevations, expanders experienced

an important enemy release and were attacked by fewer predators than natives.

Species richness increase paralleled that of mean temperature, but different changes across elevations are manifested by other network metrics. At low and intermediate elevations, neither GenSD nor VulSD increased with temperature, and both temperature and GenSD increased at high elevation, with new incoming species having broader diets than the natives. This increase in species richness supports the idea that, despite climate change being expected to reduce the number of species globally, species richness can increase locally [39,40]. At least at our temporal resolution, extinctions have not occurred, supporting findings that state that the mechanisms that cause climate-induced extinctions are not instantaneous [11,41–45].

There is increasing evidence that different taxonomic groups show different elevation responses to changing climatic conditions [20,46]. Most expanders were prey species down in the food web, mostly birds. This contrasts with other studies [15] showing that birds responded least in terms of elevation shifts than other taxonomic groups. Most basal species in our food webs reproduce annually, have a diet based on insects and/or plants, and share most predators. But birds might be more mobile than small mammals [47], and their responses to warming include the establishment of introduced species outside their endemic climatic ranges [38,48,49].

Expanders are species visiting new environments, and may survive if they find a suitable habitat, they find enough resources and/or predation pressure is not too strong. Expanders did not have wider diet

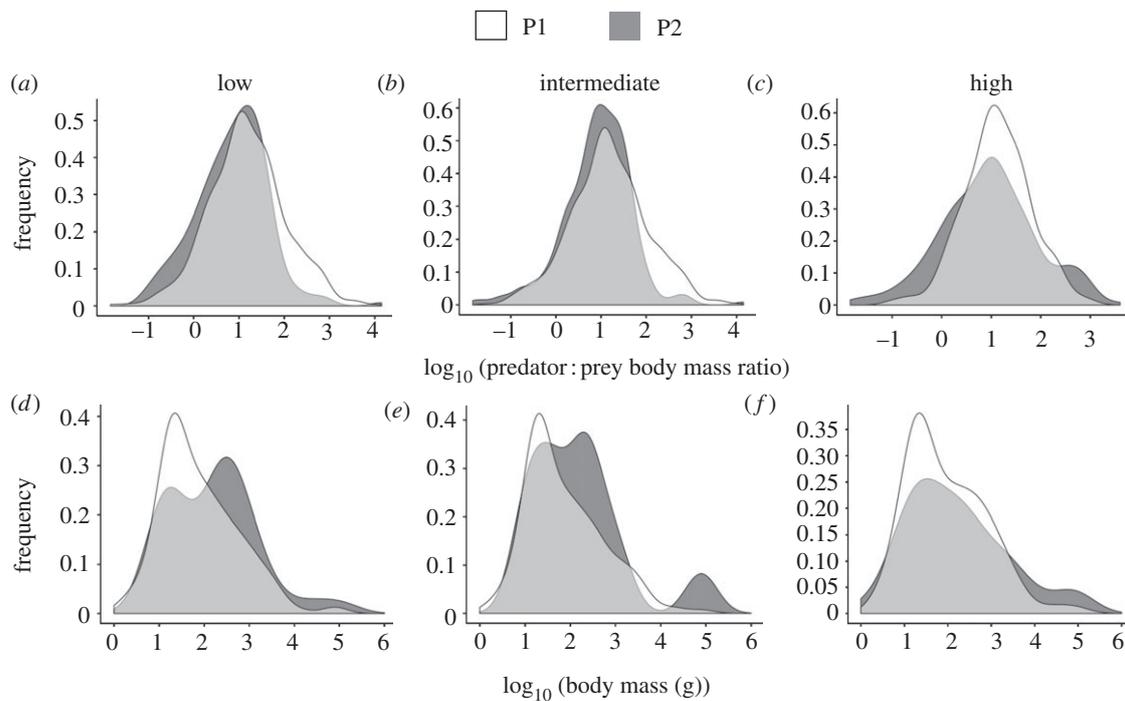


Figure 3. (a–c) Comparison of PPMR probability distribution of the food webs from P1 (1984–1990) and the food webs from P2 (1991–2001) at each elevation range; (d–f) Comparison of body mass probability distribution of new prey incomers in the period P2 (1991–2001) and native prey species already present in P1 (1984–1990) at each elevation range.

breadths than non-expanders, but they were larger and were attacked by fewer predators. The first pattern disagrees with studies stating that more generalist consumers are good candidates to firstly move upwards [24,46,50]. Actually, specialists are considered particularly vulnerable to extinction as a result of environmental change [50–53]. The lack of inequality found can be a consequence of living in an extreme and extremely fluctuating habitat, with species forcedly adapted to a relatively highly diverse diet. More diet breath can be a good predictor only for certain taxonomic groups [30].

Concerning the effects of predators, expanders had significantly fewer predators than non-expanders (mean values of 2.2 versus 3.9, respectively). This agrees with the enemy-release hypothesis. A species with few predators expanding its range is likely to find new environments with no or fewer predators, and so the establishment in this new habitat has more probabilities of success.

The analyses of standardized indegree and outdegree distributions support these results and provide an additional dimension. Our results show that consumers with relatively wide but lower diet breaths than native species and, more importantly, with a lower predation pressure, are the best suited to expand their ranges. Expanders were also more habitat specialists. As for diet breath, the explanation might rely on environmental conditions. Some species that live at the highest elevations have adaptations to cope with different environmental conditions in winter and summer. For instance, many of them make seasonal elevation migrations, and so they must be habitat generalists to some extent to survive in a completely different environment. Incoming species should not need to have these pre-adaptations to extremely changing

environments, and so they do not need to be such habitat generalists. An alternative or complementary explanation is based on the fact that specialists are more efficient in exploiting resources than generalists. So, a relatively more specialist—but still quite generalist—species could be favoured in new environments.

Basal expanders had significantly larger body sizes than non-expanders. While warming generally reduces body size within local communities [50,54,55], it is not clear whether large body-sized species tend to shift or expand their ranges more easily than smaller ones [24]. It is worth noting that species at higher trophic positions were homogeneously distributed across elevations; so range expansions in these groups would not occur.

The decrease of PPMR at low and intermediate elevations was due to larger prey species moving upwards. This might have important dynamic consequences. PPMR are proxies of interaction strengths, mostly in aquatic food webs [56], ultimately determining food web dynamics. If smaller body mass ratios imply weaker interaction strengths, we should expect mountain ecosystems to be less top-down controlled in the near future. The reported mechanism behind loss of top-down control in our study differs from those reported elsewhere in this issue [57].

The complexity of the food web analyses presented here, expanding many years to detect evidence in natural systems of climate change effects, requires an alternative way of building the food web (see [58] for a similar approach). Because interactions cannot be directly assessed in such food webs due to the impracticability of determining the diet of all species at each altitude each year, all feeding interactions come from aggregating individual species' diets, and do not change over time unless the two interacting partners

do not co-occur in a given habitat at a given elevation in a given year. Our approach, for example, does not allow for dietary shifts of expanders into their new environments. However, our database includes all found interactions at different environments and elevations; so it covers a wide range of species. Hence, it is unlikely, but possible, that a new potential interaction between a range consumer and a native resource is not already contemplated in our database.

5. CONCLUSIONS

The Pyrenees are showing some responses to climate change that could be representative of what is happening in other mountain ecosystems worldwide, i.e. the appearance of communities with novel species combinations. These novel communities are characterized by a higher proportion of larger basal prey species, mostly birds. The evidence that most incoming species come from lower elevations clearly indicates that, in the long term, if climate change continues at a similar rate, the vertebrate community at the highest elevations will become more similar to that at lower elevations. If range contractions occur at low elevations [58], and inhabiting species at the highest elevations are forced to move upwards, species extinctions in mountain environments are likely to occur in the intermediate–long term. Our study suggests that the level of climate warming that has already taken place in the Pyrenees is sufficient to have also generated changes in its size-structure and food web properties, which could have profound impacts on community dynamics, biodiversity maintenance and ecosystem functioning. Alpine communities are likely to keep changing in the next decades or centuries, probably exacerbating the patterns of change reported here.

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