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Review

High Variability Is a Defining Component of Mediterranean-Climate Rivers and Their Biota

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Abstract: Variability in flow as a result of seasonal precipitation patterns is a defining element of streams and rivers in Mediterranean-climate regions of the world and strongly influences the biota of these unique systems. Mediterranean-climate areas include the Mediterranean Basin and parts of Australia, California, Chile, and South Africa. Mediterranean streams and rivers can experience wet winters and consequent floods to severe droughts, when intermittency in otherwise perennial systems can occur. Inter-annual variation in precipitation can include multi-year droughts or consecutive wet years. Spatial variation in patterns of precipitation (rain vs. snow) combined with topographic variability lead to spatial variability in hydrologic patterns that influence populations and communities. Mediterranean streams and rivers are global biodiversity hotspots and are particularly vulnerable to human impacts. Biomonitoring, conservation efforts, and management responses to climate change require approaches that account for spatial and temporal variability (including both intra- and inter-annual). The importance of long-term data sets for understanding and managing these systems highlights the need for sustained and coordinated research efforts in Mediterranean-climate streams and rivers.

Keywords: Mediterranean streams and rivers; seasonality; inter-annual variability; management; fish; macroinvertebrates; biomonitoring; conservation

1. Introduction

Varying levels of temporal and spatial variability characterize all natural stream and river ecosystems, and are key factors in determining patterns and processes at the population, community, and ecosystem levels [1–5]. At the temporal scale, intra- (i.e., seasonal) and inter-annual variability in precipitation and temperature, and the former's influence on flow dynamics, play a central role in population dynamics and community composition in most climatic regions of the world [6–8]. At the spatial scale, spatial variability in precipitation and temperature patterns combined with topographic variation lead to spatial variation in hydrologic patterns.

Mediterranean streams and rivers, however, present a significantly greater level of seasonal and inter-annual variation compared to some other humid-climate rivers, where more stable conditions prevail [9,10]. High inter-annual variability in precipitation and associated variability in flow dynamics is characteristic of Mediterranean-climate regions [11,12]. For example, over a period of nine years, mean annual flow observed in several small streams in northern California, USA ranged 0.2–6 times their long-term average [13]. Temperatures also vary seasonally in Mediterranean-climate regions but over a smaller range of magnitudes relative to precipitation. Winter temperatures are generally mild (7–13 °C) with infrequent frosts and snow, whereas summers are typically hot, with a mean temperature of 14–25 °C (e.g., [14]). Temporal and spatial variation in abiotic factors have been reviewed in detail in [10] and [11]. The high variability in flow dynamics includes flow intermittency as a typical characteristic of many Mediterranean streams. For instance, non-perennial streams represent 50% of the stream network in Greece [15] and 66% in Southern California, USA [16].

Despite the evolutionary history of each Mediterranean-climate region has shaped distinct regional biodiversity patterns in terms of species richness and composition [17], the high temporal variability generates similar seasonal and inter-annual patterns. Seasonal variability in Mediterranean-climate regions is highly predictable [10,18] and generates pronounced biological differences between the wet and the dry seasons (e.g., [11,19,20]). The onset and duration of the wet and dry seasons are, however, widely variable (both spatially and from year to year) with potentially large effects on populations and communities. For example, in intermittent streams, the onset of the dry season coincides with the decline and loss of hydrological connectivity and habitat availability [11]. The onset timing determines the duration of the dry season, which directly influences the degree of seasonal change in biotic communities, as taxa adapted to flowing conditions are progressively replaced by those more tolerant to drought. Relative to flow seasonality, inter-annual flow variation in Mediterranean streams is less predictable and the effects of multi-year drought or wet periods can have prolonged and irreversible consequences. For example, a five-year prolonged drought was shown to prevent the recovery of biotic communities to the pre-drought reference state [21]. The sensitivity to severe drought varies spatially and is especially relevant for intermittent rivers where aquatic species can be completely extirpated, unlike perennial rivers in which post-drought recovery occurs fairly rapidly [21,22]. In other ways, however, Mediterranean-climate river communities are more resilient to the effects of wet and dry years than rivers located in other climatic regions, owing to biological adaptations to seasonal variability that may confer greater resilience to inter-annual variability in flows [23,24].

The high temporal variability of Mediterranean streams and rivers presents challenges for ecosystem management. For example, spatial (intermittent vs. perennial) and temporal (seasonal and inter-annual) variability in communities and populations complicates the interpretation of biological monitoring approaches used to assess water and environmental quality, especially in intermittent streams [25,26]. However, the ability to detect anthropogenic impacts on flow and aquatic communities becomes increasingly difficult with increasing variability in natural environmental conditions. This underscores the importance of long-term data to evaluate trends and drivers of ecological change in Mediterranean streams and rivers.

In this article, we argue that flow variability and associated ecological characteristics are not only much higher in streams and rivers in Mediterranean-climate regions compared to those in most other parts of the world, but also that this variability is a defining element of these unique ecosystems. We first describe the temporal and spatial variability of climate conditions that influence the pattern and distribution of flow regimes in Mediterranean-climate regions worldwide, comparing the Mediterranean Basin, California, Chile, South Africa and southern and southwestern Australia. Second, we review the inherent seasonal and inter-annual variability in Mediterranean rivers and its influence in shaping populations and communities, focusing on macroinvertebrates and fish, while also exploring spatial variation within and among regions. Finally, we analyze management implications of this variability on biomonitoring and conservation management of Mediterranean streams and rivers.

2. Variability in Abiotic Environmental Conditions

Moderate seasonal changes in temperatures coupled with high seasonal and inter-annual variability in precipitation distinguish Mediterranean-climate regions from other climate regions of the world [11]. For example, Dettinger et al. [27] reported that inter-annual variation in annual precipitation was 3–7 times greater in California than observed in the eastern United States. Despite the uniqueness of Mediterranean-climate regions, there is substantial variation in abiotic environmental conditions both within and among them. Using geographic boundaries of Mediterranean-climate regions consistent with those defined in [10], distinct spatial patterns in topographic and climatic conditions within each region are evident (Table 1).

Table 1. Elevation and climate characteristics for the five Mediterranean climate regions from the world, derived from the SRTM 90 m Digital Elevation Database, v4.1 [28] and Worldclim Database, v1.4 [29]. For each variable, the mean value and standard deviation (SD) of values from all data points within a region are reported. The temperature and precipitation records are from the period 1960–1990.

Region	Mediterranean Basin	California	Chile	Australia	South Africa
Area (km^2)	2,137,100	324,900	148,400	791,300	123,100
Elevation (mean ± SD m.a.s.l.)	640 ± 490	800 ± 580	980 ± 580	200 ± 185	530 ± 461
Mean temperature (mean ± SD °C)	15 ± 3	13 ± 4	13 ± 3	17 ± 2	16 ± 2
Mean min. temperature [1] (mean ± SD °C)	2 ± 3	0 ± 4	3 ± 4	5 ± 1	4 ± 2
Mean max. temperature [2] (mean ± SD °C)	31 ± 4	30 ± 5	24 ± 4	32 ± 3	28 ± 3
Annual precipitation (mean ± SD mm)	560 ± 250	700 ± 410	420 ± 520	390 ± 165	430 ± 200

Notes: [1] Minimum temperature of coldest month; [2] Maximum temperature of warmest month.

The Mediterranean Basin occupies the largest land area of the Mediterranean-climate regions worldwide, followed by Australia, California, Chile, and South Africa. Mean elevations for Mediterranean regions are between 500 and 1000 m.a.s.l., with the exception of Australia, which averages 200 m.a.s.l. and has lower topographic relief relative to the other regions (Figure S1). Elevations tend to increase from coastal zones to the interior of Mediterranean-climate regions. With its coastal mountain ranges and large interior Central Valley, California's topographic patterning is notably distinct from other Mediterranean-climate regions (Figure S1).

Mean annual temperatures are similar for all Mediterranean-climate regions (13–17 °C). The minimum and maximum temperatures in the coldest and warmest months, respectively, are also similar among regions (Table 1). Spatial variation in temperatures largely reflects topographic gradients, with decreasing annual temperatures occurring at higher elevations (Figure S2). The Mediterranean-climate regions show distinct spatial patterns in seasonal variation in monthly temperatures (Figure 1). For example, South Africa, Australia, and Chile display less seasonal variation in monthly temperatures relative to that of California and the Mediterranean Basin (Figure 1).

There is greater variation in precipitation than temperature among the Mediterranean-climate regions (Table 1). California receives the highest annual precipitation on average (700 mm), followed by the Mediterranean Basin (560 mm). Chile and South Africa receive over 400 mm of precipitation a year on average, while Australia receives less than 400 mm a year. Spatial patterns in mean annual precipitation generally follow latitudinal gradients, with increasing precipitation at higher latitudes (Figure S3). However, there are also notable effects of topography giving rise to spatial variation, especially in California and the Mediterranean Basin, with higher elevations receiving greater precipitation [12]. Topographic effects on precipitation are less pronounced in Chile, South Africa, and Australia. Seasonal variation in monthly precipitation also varies among regions and spatially within regions (Figure 2). California and Chile display the greatest overall variation in season precipitation compared to the Mediterranean Basin, South Africa, and Australia. Regarding spatial variation within regions, areas of higher precipitation variability tend to occur in more arid zones (e.g., northern Chile) and parts of the Mediterranean Basin in North Africa and the Middle East.

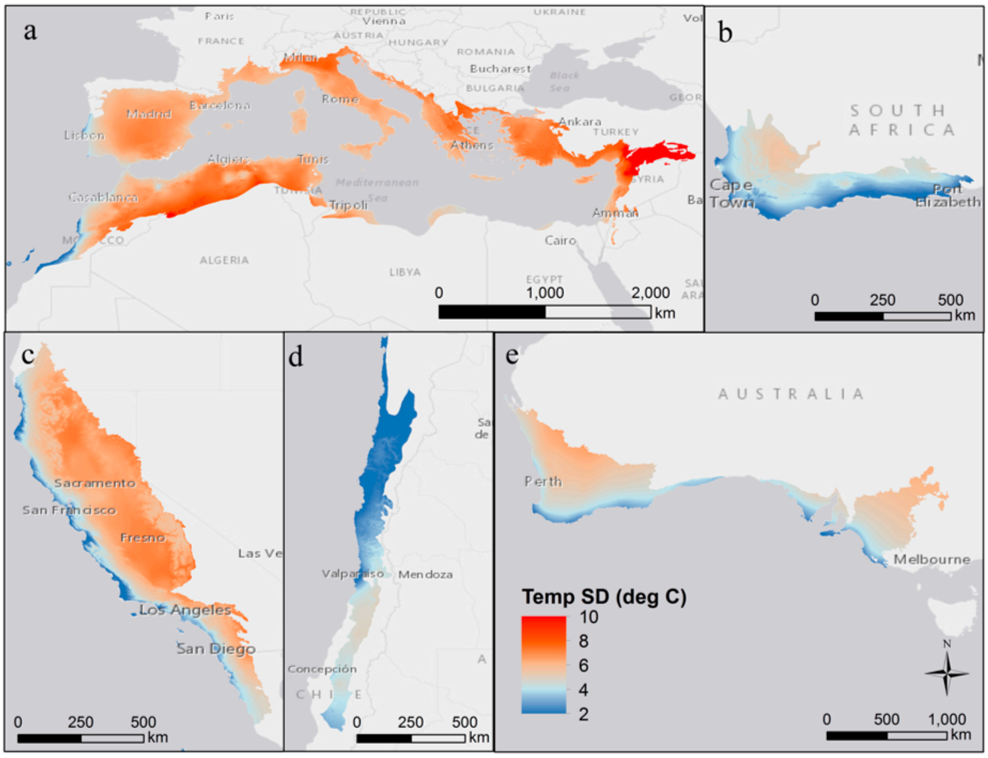

Figure 1. Seasonal variation in mean monthly temperatures (SD) for the five Mediterranean regions of the world: Mediterranean Basin (**a**); South Africa (**b**); California (**c**); Chile (**d**); and Australia (**e**). Data source: Worldclim Database, v1.4 [29]. Records correspond to the period 1960–1990.

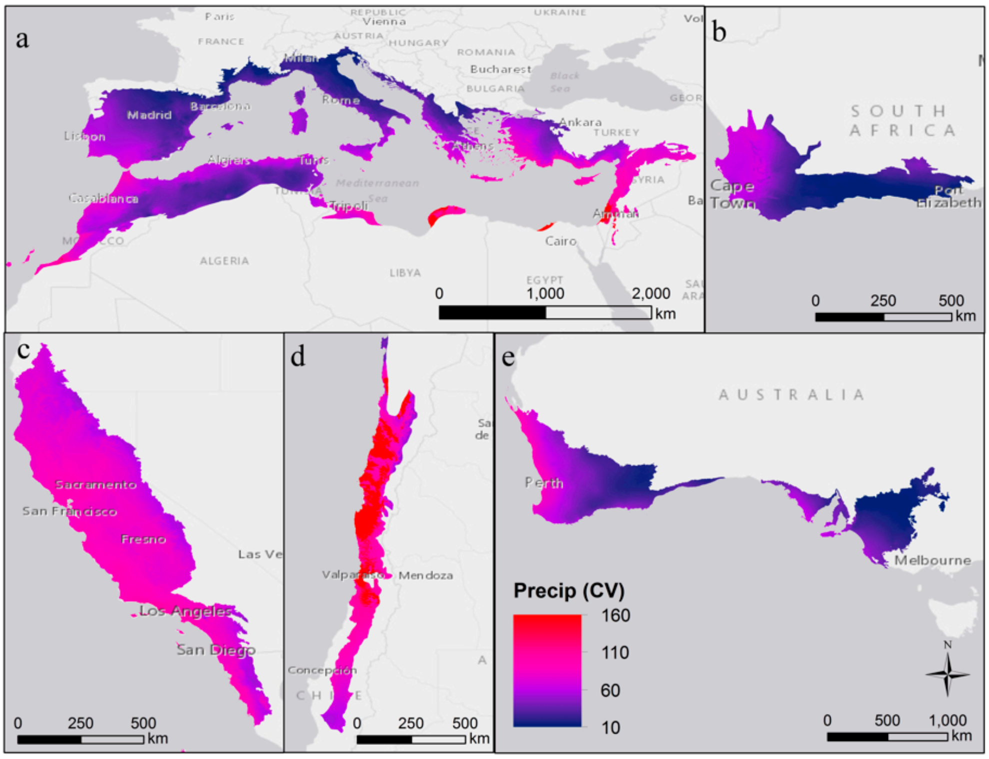

Figure 2. Seasonal variation in mean monthly precipitation (CV) for the five Mediterranean regions of the world: Mediterranean Basin (**a**); South Africa (**b**); California (**c**); Chile (**d**); and Australia (**e**). Data source: Worldclim Database, v1.4 [29]. Records correspond to the period 1960–1990.

The strong spatial and temporal variation in climatic and topographic characteristics within and among Mediterranean-climate regions has direct influences on the pattern and distribution of flow regimes. In California, for example, 2/3 of annual runoff is conveyed by streams in the northern 1/3 of the state [27]. Stream flow regimes are also highly influenced by topography, including orographic effects and the proportion of precipitation falling as snow, which gives rise to spatial variation within regions. For example, the Salmon River (drainage area: 1950 km^2) in northern California has mean annual runoff of 815 mm and has a mixed rainfall-snow runoff regime, with peak flows (>500 cubic meters per second (cms)) in the early winter and high flows (>100 cms) extending through the early summer, followed by steady summer baseflows into the fall (5–10 cms) (Figure 3). In contrast, Orestimba Creek (drainage area: 350 km^2), located in a rain shadow on eastern side of the California's coast range has an annual runoff of only 40 mm. It flows intermittently from December through May with rainfall runoff and is predictably dry the rest of the year. Santa Cruz Creek (drainage area: 200 km^2) is located on the coast of southern California. It conveys 90 mm of runoff per year, with flow patterns driven by rainstorms concentrated in the wet season. All three streams show strong seasonality and notable inter-annual variability in both the timing of peak flows and duration of the low-flow period (Figure 3).

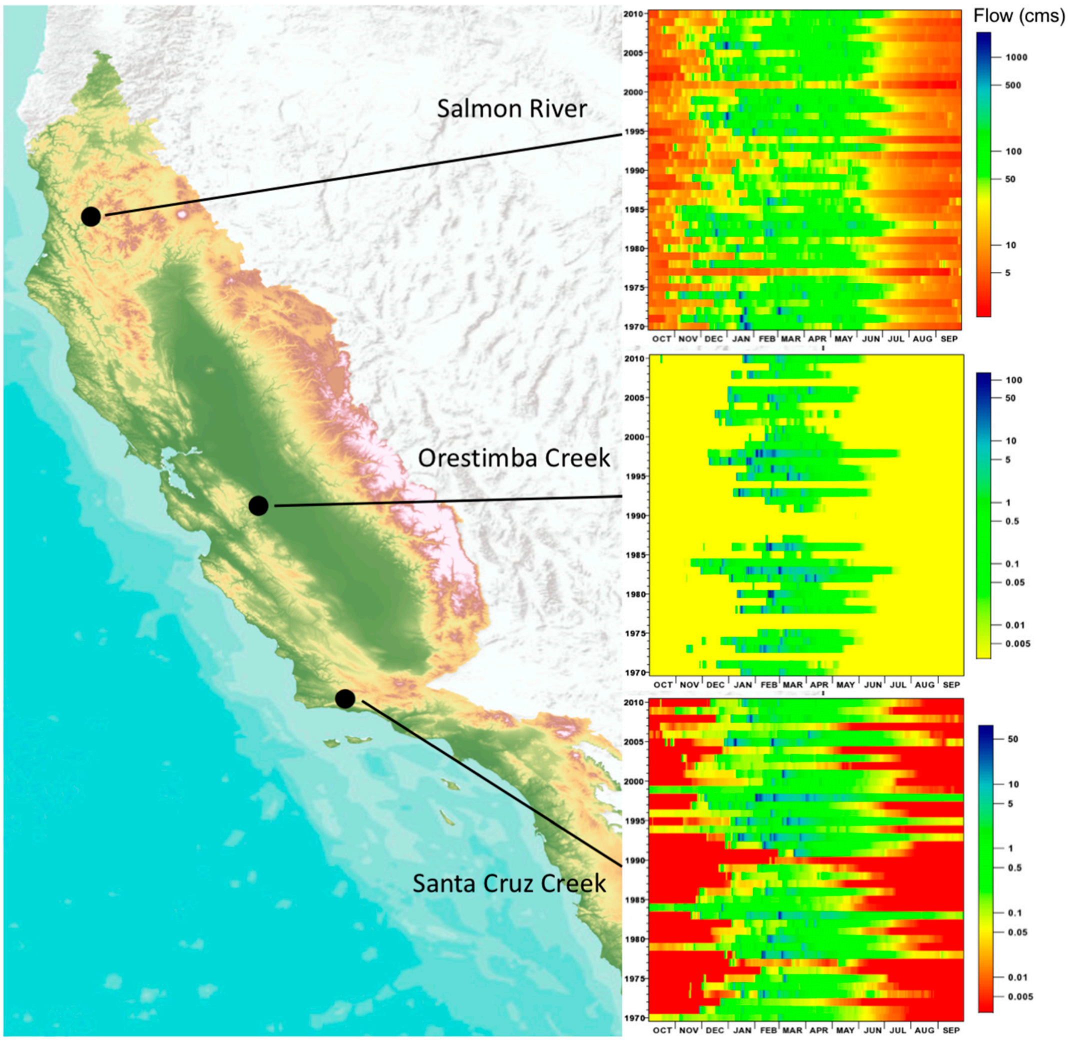

Figure 3. Daily discharge (cms) at Salmon Creek (USGS Gage 11522500), Orestimba Creek (USGS Gage 11274500), and Santa Cruz Creek (11124500) reveals spatial variation within the Mediterranean climate region of California. Records from 1970 to 2010 show inter-annual variability and strong seasonality in discharge.

Climate models predict that frequency, duration, intensity, and spatial extent of extreme weather events, including floods and droughts, are likely to increase worldwide associated with anthropogenic climate-warming [30]. Seasonality of rainfall is also predicted to shift under future climate regimes [31]. However, relative to predictions of future warming, modeled projections of precipitation remain highly uncertain for mid-latitude zones, including Mediterranean regions of the world [32]. Nevertheless, semi-arid and arid regions of the world, including the Mediterranean Basin and western US, are generally expected to face decreasing water availability as a result of climate change. Using a global scale hydrologic model with 2050 climate projections under high emissions scenarios (A2), Döll and Schmied [33] indicate that summer low-flows, in particular, are susceptible to declines. Moreover, they postulate that transitions from perennial to intermittent flow regimes could be expected in Mediterranean rivers and streams, most notably in California and around the Mediterranean Basin, but also in South Africa, Australia, and Chile.

Climate variability is expected to increase under climate change and Mediterranean regions may concurrently face a growing risk of both drought and flooding. In California, for example, there is a growing likelihood of multi-year drought [34] and of extreme rain events [35]. Furthermore, a growing proportion of precipitation is expected to be delivered in a few large storms and less by smaller, more frequent storms [36], potentially reducing the recharge of shallow and deep groundwater sources critical for sustaining stream baseflows. Consequently, the summer low-flow period for many streams in California is likely to increase in both duration and intensity in the future. For all Mediterranean regions of the world, reduced and more variable water supplies would likely intensify human demands for surface water in rivers and streams, particularly in the dry season, potentially accelerating the depletion of flows and associated impacts to biotic communities.

3. Biological Variability in Mediterranean-Climate Rivers

3.1. Population Variability

3.1.1. Macroinvertebrate Populations

Within years, Mediterranean streams can display remarkable variation in environmental conditions, experiencing extremely wet winters and consequent floods to severe droughts when atypical intermittency can occur. With severe floods, macroinvertebrate populations decline, especially for univoltine populations dominated by single or closely related age classes. Generally, the higher the frequency and magnitude of floods the greater the reduction in abundance of particular taxa [11]. For example, the effects of floods in the Matarraña River, Spain, caused the reduction in 97% of Ephemeroptera and Plecoptera populations; individuals that survived shifted their dietary preferences as a result of adaptation to limited food resources after disturbance [37]. Such strategies of endurance or avoidance of floods determine population recovery after floods in Mediterranean streams [24].

Severe droughts can have long-term consequences for populations of benthic macroinvertebrates. Resh et al. [26] used several long-term studies from Californian streams to examine the effects of droughts on benthic macroinvertebrates. For example, shifts in population age structure can occur as populations recover after severe drought [38,39]. These can result from intrinsic population phenomena, such as timing of population recolonization following habitat recovery, or from biotic interactions [26]. Moreover, when populations increase because typical flow-induced mortality does not occur during severe drought years, intense intraspecific competition may lead to reduced fitness of the population, as demonstrated for the caddisfly *Helicopsyche borealis* in a Mediterranean-climate California stream [40].

Many macroinvertebrate populations, however, are highly adapted to the strong seasonality characteristic of Mediterranean-climate streams, and have developed unique strategies for coping with or avoiding drought stress, especially those inhabiting intermittent streams. For example, some stoneflies (e.g., *Guadalgenus franzi*, *Hemimelaena flaviventris*, and *Isoperla curtata*) from intermittent-streams in the southern Iberian Peninsula undergo nymphal or egg diapause during the dry period [41]. Similarly, the caddisfly *Mesophylax aspersus* exploits temporary waters as larvae and the adults undergo summer diapause, using caves as temporal refugia while delaying reproduction until flow resumption [42].

Populations may also show high inter-annual variability. For example, in a springbrook in Northern California, densities of the caddisfly *Gumaga nigricula* dropped from thousands/m^2 to zero during a period following recovery from a several drought and after 10 years although the age structure recovered, densities were far lower than during pre-drought conditions [39]. Feminella and Resh [40], in a Californian stream, reported on average over a two-fold difference in densities for the caddisfly *Helicopsyche borealis* for wet years compared to dry years and over a four-fold difference for wet years compared to drought years. Many community level studies conducted over multiple years also have documented significant variation in population densities over time (e.g., [21]).

3.1.2. Fish Populations

The abundance patterns of stream fishes in Mediterranean systems vary considerably among species [22]. Some abundance declines are strongly linked to flow conditions, including both floods [43] and droughts [22], although declines of individual species may have little effect on assemblage structure.

Fish population responses to environmental variability have been quantified by exploring the interactions between life history requirements and flow and habitat parameters [44,45]. For example, two common cyprinid species in a Mediterranean river in southwestern Portugal (Chub *Squalius torgalensis* and nase *Chondrostoma lusitanicum*) showed differences in their life histories related to flow conditions, which highlighted the interplay of life history and environmental variability in fish population dynamics in rivers in Mediterranean-climate regions [46]. Flow permanence is one of the most important determinants of fish population and assemblage structure and significant differences exist in population fish dynamics between intermittent and perennial Mediterranean-climate streams [44,47]. For example, larval fishes occurred earlier in intermittent streams than perennial streams in California, possibly as a result of the warmer temperatures, which may increase survival rates from the increased growth opportunities [47]. Variable growth opportunities among streams contribute to trait diversity at the scale of populations, and potentially enhance stability as reported for salmon populations in California [48].

Studies of survival of stream fishes in Mediterranean-climate river systems are few, although this is changing. Survival can be estimated by tracking changes in abundance through time, although differences in counts through time can be confounded by movement of individuals into and out of the study system. Therefore, most studies have focused on the dry season, when movement rates are generally low (e.g., [49]), and on intermittent streams where movement is impossible once riffles become dry and the stream fragments into a series of isolated pools. The survival of threatened juvenile steelhead trout (*Oncorhynchus mykiss*) was studied across nine years in four intermittent streams in Mediterranean climate California, showing that mean over-summer survival was 30% [13]. This suggested that the dry summer-season could be a bottleneck period for juvenile salmonids. Moreover, inter-annual variation in the over-summer survival of trout was related to both the magnitude and duration of summer low flows, providing a critical link between population dynamics and flow variability. Similarly, a recent study on *O. mykiss* in an intermittent California stream found that over-summer survival was positively correlated with cumulative precipitation of the previous winter [50]. In addition, in Mediterranean-climate California, Woelfle-Erskine et al. [45] examined over-summer survival of imperiled juvenile coho salmon (*O. kisutch*) and steelhead trout and found that species-specific differences in juvenile distributions influenced the abiotic conditions that over-summering salmon and trout were exposed to, and hence the factors that governed over-summer survival.

Merciai [51] provides a rare example of a study estimating survival across seasons (although not years). A mark-recapture study was conducted to explore the survival of two threatened cyprinid fishes (barbel *Barbus meridionalis* and chub *Squalius laietanus*) in the Tordera Basin, Catalonia, Spain.

They explored how season, flow, water temperature, and pool depth influenced abundance and survival patterns in perennial compared to an unnaturally intermittent reach (from diversions) across a one-year period. A clear effect of diversions on the abundance and survival of both chub and barbel was observed, and fish abundance and survival was generally higher in the perennial reaches with high flow, lower temperature, and deeper pools compared to the intermittent reach. They also report that apparent survival was depressed during the winter (November–January) and during late spring (May–July) relative to the dry summer season, and they attribute these results to movement during the wet season and for spawning, respectively. This result emphasizes the challenge of distinguishing the effects of movement from mortality when estimating fish survival in highly seasonal, Mediterranean streams.

Movements, both emigration during river contraction and immigration during river expansion, have the potential to strongly influence population dynamics of Mediterranean stream fishes. Spawning migrations are common among native fishes (e.g., [52–54]), whereas other movements appear to be associated with adaptive behaviors to seek refugia or to colonize/re-seed habitats after severe droughts or floods (e.g., [49,55]). These latter movements may be may be especially important in Mediterranean systems with large seasonal and inter-annual variation in the magnitude, frequency, and duration of droughts and floods, which are areas where the distribution and quality of the available refuge pools can strongly influence the dynamics, persistence, and recovery of stream fishes [56,57].

Taken together, these studies highlight that patterns of reproduction vary among species and that survival and movement vary across both seasons and years, with growing evidence that fluctuations are linked to flow variability and associated variability in physical habitat conditions.

3.2. Community Variability

3.2.1. Macroinvertebrate Communities

Community changes between the wet and the dry season in Mediterranean-climate regions have been reported for many aquatic organisms, including microbes (e.g., [58]), phytoplankton (e.g., [59,60]), benthic algae (e.g., [61–63], macroinvertebrates (e.g., [19,64,65]), and fish (e.g., [44,47,63]), and for riparian vegetation (e.g., [66]). Nevertheless, macroinvertebrates are by far the most investigated group and studies on seasonal changes have focused on whole communities as well as the composition of particular taxonomic groups (e.g., Plecoptera [67]; Trichoptera [68]; or Chironomidae [69]).

Seasonal community changes in Mediterranean rivers reflect habitat changes between the wet and the dry season [65]. The onset of the dry season drives habitat changes that impose new environmental filters for aquatic communities. Riffle habitats are gradually reduced and riverbeds start to be dominated by pool habitats that are colonized by typical lentic species. If riffle habitats disappear, isolated pools are composed by communities that, over time, diverge from the original ones depending on local factors and stochastic processes [70] (Figure 4). If pools eventually dry up, lentic species disappear or become part of the river seedbank [24,57]. At the end of the dry period, flow resumption restores riffle habitats imposing new constraints for lentic species and promoting the re-colonization of riffle ones.

The degree of seasonal changes vary spatially and are more evident in Mediterranean rivers experiencing flow intermittence than in perennial ones, even when they are of similar sizes [20] (Figure 4). Despite taxonomic richness usually being similar between the wet and the dry season in both perennial and intermittent rivers [20,71], with some exceptions [72], density, biomass, and diversity typically vary. Higher densities and biomass have been found in perennial and intermittent rivers during the dry season, whereas diversity is usually higher in the wet season in intermittent rivers [20]. Taxonomic and trait composition also differs between seasons in both perennial and intermittent rivers. Seasonal changes in macroinvertebrate communities are commonly associated with a shift in numerical dominance of taxa from EPT (Ephemeroptera, Plecoptera, and Trichoptera) in the wet season to OCH (Odonata, Coleoptera, and Heteroptera) in the dry season [19,72,73]. The degree of seasonal community change tends to be greater in intermittent than perennial rivers [20,74,75], with the exception of one study that included several Iberian streams [71]. Typically, taxa with particular traits that allow them to withstand flow intermittence are found during the dry season and are especially abundant and diverse in intermittent rivers [24], which tend to support more taxa that are unique to each season, relative to perennial rivers [20].

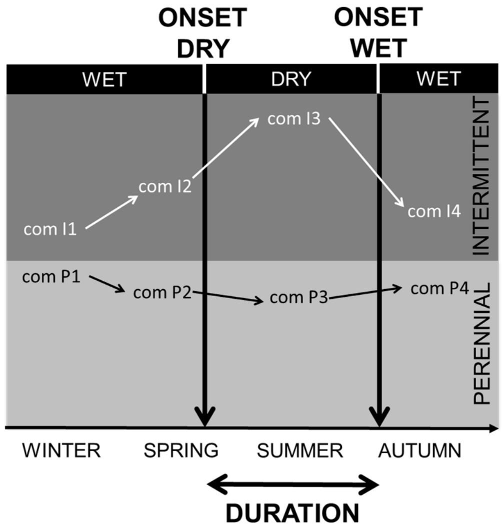

Figure 4. Diagram showing expected seasonal community changes (com I# and com P#) in relation to the onset and duration of the dry and wet periods. The slope of the arrows represents the degree of change between community pairs. The distance between com P1 and com I1 may vary depending on the local conditions (e.g., presence of refuges, geographical isolation). I: intermittent, P: perennial.

The onset and the duration of the dry and wet periods can also influence seasonal variability in biological communities (Figure 4). The onset of the dry season is a critical time that can result in dramatic consequences for communities in Mediterranean-climate streams and rivers. Many macroinvertebrates in these systems have their life cycles synchronized with the onset of the dry period (e.g., [41]). Therefore, an early or a later drying period can lead to significant community changes.

Studies conducted in temperate intermittent rivers have found that communities are highly nested with flow duration (i.e., taxa found in more intermittent rivers are subsets of those found in less intermittent or perennial rivers; [76,77]), suggesting that there is a negative relationship between the duration of the dry season and seasonal community changes. Supporting this pattern, Bêche et al. [19] showed that intermittent rivers in years with longer dry periods had lower taxonomic and functional differences than in years with shorter dry periods. Leigh et al. [78], however, in a study relating temporal changes in intermittent rivers across different climate regions (arid, Mediterranean, and temperate regions) found that the duration of the dry period did not cause temporal community changes from those measured before to those measured after the dry period. Additional studies that analyze how the onset and the duration of the dry season affect communities in Mediterranean-climate region rivers are needed, especially under future climate change scenarios [79].

Long-term studies analyzing inter-annual variability of macroinvertebrate communities in Mediterranean streams and rivers are rare. There are few datasets available that include more than 10 years of data, which are needed to detect long-term community changes (cf. [26,80,81]). Many of these datasets have been used to relate inter-annual community-changes to climate change, highlighting that the frequency of dry years has increased in more recent years and that communities have changed accordingly. For example, Sáinz-Bariáin et al. [82] found an increase in Trichoptera richness in high-altitude, mountain Mediterranean rivers after a 20-year period, whereas Pace et al. [81] found that riffle species shifted to lentic species during a 14-year period in two Mediterranean streams with different hydrological characteristics. These patterns follow the hydrological changes experienced in these areas that may be the result of a changing climate. Comparisons between wet and dry years have shown that richness and exclusive species are higher in wet than in dry years, which has been related to relatively higher habitat availability in wetter years [83]. However, other studies did not observe these differences in macroinvertebrate richness [21]. For macroinvertebrate density, no significant differences between wet and dry years are reported [21,84].

Inter-annual community changes in rivers and streams in Mediterranean-climate regions are sometimes less obvious than those reflecting seasonal changes [26]. For example, some authors found that macroinvertebrate communities differed more between seasons than among three consecutive years [73,84]. These small community changes, however, have been significantly related to comparing wet-with-wet and dry-with-dry years [21]. Wet years are dominated by species adapted to high flows, whereas dry years include a higher proportion of lentic species [85]. Inter-annual community changes can interact with seasonal changes, resulting in differential effects under varying times of onset and the duration of the wet and dry seasons. For example, Bêche et al. [21] found that macroinvertebrate differences between perennial and intermittent rivers were greater during dry than wet years.

3.2.2. Fish Communities

Results from several studies that focused on seasonal shifts in fish communities of Mediterranean-climate rivers emphasized that fish species shift their distributions at different spatial scales in response to seasonal changes in flow and habitat availability. These shifts occur both at the reach scale [86,87] and the microhabitat scale [88,89]. In contrast, the few studies that have explored variation in fish assemblages across seasons found no significant differences in diversity [86] or fish assemblage structure [90], despite considerable variation in environmental conditions among seasons. However, Alexandre et al. [91] explored seasonal variation in fish assemblages from regulated and non-regulated rivers in a temporary and permanent Iberian system, and found higher variation in non-regulated than regulated systems, and higher seasonal variation in the temporary system examined compared to the permanent one. The changes in fish communities in the temporary systems, however, were mainly related to the presence of exotic species, which hinder natural community patterns from forming.

In terms of inter-annual variability in fish communities, Magalhães et al. [22] sampled fish from 1991 to 1998 in the Torgal Basin in southwestern Portugal. Eight sites were distributed longitudinally and each was sampled after the rainy period but before the summer dry down. The degree of fluctuation in population abundance differed among species: abundance patterns were moderately stable for common species (cyprinids, chub and nase) but fluctuated greatly for rare (e.g., *Gasterosteus* sticklebacks and *Anguilla* eels) and non-native species (*Gambusia* and *Micropterus* bass). These results suggest fluctuations within the species pool, even among some native species that have been selected by these conditions. Despite the fluctuations in individual species, however, there were few changes in species composition or in their rank abundance across years at the basin scale. Both drought and high rainfall springs were drivers of assemblage change, but the assemblage was resistant to drought and recovered the earlier assemblage structure shortly after the cessation of drought conditions. Similarly, Matono et al. [92] reported that fish assemblages in two intermittent streams in south Portugal were stable and resilient over a 4–11 year period (depending on the site) despite considerable inter-annual variation in rainfall patterns. However, the assemblages were much less stable at sites with high human disturbances (e.g., high nutrient/organic loads, sediment loads).

Bernardo et al. [93] examined changes in fish communities in the Guadiana River in southern Portugal from 1980 to 1999 at 40 sites distributed throughout the basin, including low- to high-order streams. They reported considerable inter-annual variability as well as directed changes following extreme drought and flood events. Notably, they emphasized that non-native species (namely green sunfish, *Lepomis cyanellus*) were able to expand their distribution during a multi-year drought. Green sunfish represented ~83% of the total assemblage at one point, but that this trend was reversed following years with above-average flows and several flood events, which greatly increased the contribution of native fishes, particularly non-rheophilous species. Similarly, Bêche et al. [21] showed that a native cyprinid (California roach, *Hesperoleucus symmetricus*) declined following an extreme multi-year drought in California based on annual abundance data collected over 19 years in two streams. However, in contrast to the results of Bernardo et al. [93], roach failed to recover following the cessation of drought, possibly as a consequence of non-native green sunfish withstanding displacement/mortality during subsequent flood events and becoming permanently established at one study site during the multi-year drought. Overall, the results of these two studies suggest that the persistence of native fishes might rely on large flow events in highly invaded Mediterranean-climate rivers, but that biotic factors also play a role.

Another long-term study of note has focused on the stream fishes of Putah Creek (Davis, California, USA), which have been sampled at 6 sites distributed over 30 km of stream since 1994 [54,94]. An early observational study revealed a gradient from upstream (dominated by native fishes) to downstream (dominated by non-native fishes), and considerable inter-annual variation in the fish assemblage, with a shift towards a native dominated assemblage following wetter winters [54]. These results were subsequently used to guide environmental flow releases from the Monticello dam that were mandated as part of a legal decision [95]. Following implementation of the new flow regime, including changes to the release schedule designed to benefit native species, the community shifted to one dominated by native fishes across ~20 km of lower Putah Creek—with more stability in the community from year to year, despite considerable inter-annual variation in precipitation patterns [94]. These results emphasize the value of long-term data sets for identifying fish-flow relationships that can subsequently guide flow management in regulated rivers (a theme we revisit in Section 4.2).

Finally, stream fishes and local abiotic conditions have been sampled quarterly (except winter) in the Tordera Basin (northeastern Catalonia, Spain) since 2001. These data have been used to explore variation in fish populations and communities among seasons, sites, and years (e.g., [51]), as well as studies exploring trophic variation and fish conditions between sites, including a comparison of perennial and intermittent reaches [96]. This research has important implications because the Tordera is influenced by water abstractions and much recent research has focused on understanding the effects of such diversions on water temperature [97], the flow regime, and fish assemblage [98]. This work has revealed, for example, that sites affected by water abstraction tend to have reduced flows [97] and more variable stream temperatures [97] compared to control sites. Moreover, affected sites were characterized by reduced catch per unit effort of fishes and a shift towards more water-column and intolerant fish species [98]. This body of research highlights the value of long-term data sets for exploring the impact of anthropogenic activities after accounting for natural variation among seasons and sites.

Together, these studies highlight the value of long-term data sets for understanding how fish populations in Mediterranean-climate rivers respond to and recover from extreme events such as multi-year drought, including how responses are influenced by non-native fishes and other anthropogenic stressors (e.g., river regulation, water diversion, water treatment).

4. Variability Governing Mediterranean River Management

4.1. Biomonitoring in Highly Variable Systems

Mediterranean streams and rivers are particularly vulnerable to human impacts [10,11] despite constituting one of the global biodiversity hotspots [99]. As highlighted in the previous sections, seasonal and inter-annual variability in Mediterranean streams and rivers strongly influences macroinvertebrate and fish communities, the two groups most widely used in biomonitoring programs worldwide [100,101]. As a result, values of biotic metrics based on these groups may change drastically over different seasons and years, complicating the assessment of ecological condition and limiting their usefulness for informing management and conservation efforts [26].

Many biomonitoring programs worldwide use the reference condition approach underpinned by legislations such as the Clean Water Act in the US or the Water Framework Directive in Europe [102]. The reference condition approach represents the baseline, natural or unimpaired, condition of an ecosystem; the deviation from this condition is used to establish the level of disturbance of a water body [103,104]. This approach aims at capturing natural spatial and temporal variability of biological communities by including significant number of sites sampled at different seasons and different years to eventually obtain the characteristic "natural" conditions [104]. However, reference conditions may present several limitations as a result of its relatively static (e.g., mean value of an index and associated standard deviation) and reductionist (i.e., specific assemblages sampled within a certain time period) character of this approach [105]. This can be particularly true for high-variability systems such as rivers from Mediterranean-climate regions, in which the establishment of reference conditions has been a challenging task ([25] and references therein).

Variability in biotic metrics can differ depending on the season and the time period included in the analysis. For example, results from two long-term macroinvertebrate-based assessments conducted in four stream sites in Northern California (1984–2003) and in 171 in Catalonia (1996–2004) showed that variability was mainly attributed to the interaction between years (dry vs. wet) and seasons (spring vs. summer) for most of metrics [80,106]. In contrast, results from a three-year study (2003–2005) in 14 stream sites from Spain did not present significant inter-annual nor seasonal variability in the metrics analyzed, showing a higher stability than the streams studied in California that may be attributed to the shorter duration of the former study. Again, this highlights the need for more long-term datasets [71].

In general, the extent of inter-annual variability depends on the metrics analyzed, stream characteristics, and study-period length (Table 2). Comparing several studies in California and the Mediterranean Basin, inter-annual variability was the highest for number of EPT and the Northern Coastal California Index of Biotic Integrity (IBI) in non-perennial streams from California during summer across a 20-year period [80]. In contrast, the lowest inter-annual variability was observed for the Iberian Biomonitoring Working Party index (IBMWP) and ICM-11 multimetric index in perennial siliceous streams from Spain across three years [71]. This reinforces the idea that shorter periods may present higher stability and precision, in agreement with [26] who reported less precision in setting reference conditions when data longer than six years were included.

In the study from Mazor et al. [80], the spatial component interacting with year, however, represented the highest source of variability for the IBI index and was mainly associated with the degree of flow intermittence and stream order. Compared to perennial Mediterranean reference streams, intermittent ones present much higher variability in assemblages and biotic indices, complicating the validation of the reference condition criteria using biological communities across space [25,106–109].

A failure to distinguish among the different hydrological regimes (i.e., perennial, and intermittent) in Mediterranean streams and the distinct faunas present in each can confound assessments of ecological status when using macroinvertebrates as indicators [64,109]. In South Africa, Watson and Dallas [110] found disproportionate representation of tolerant taxa in undisturbed ephemeral streams, limiting the use of current South African standardized biomonitoring protocols. Likewise, in Australia, Bunn [111] reported that predictive models such as RIVPACS performed well for perennial streams, but were less reliable when applied to intermittent streams. Recently, results from biomonitoring program for the period 2005–2010 in southwestern Australia showed that the AUSRIVAS model [112] might present limitations in distinguishing natural from human disturbances, especially because of the high variability in reference streams with fluctuating flow [113].

In addition to the failure of indices to be accurate in intermittent streams in Mediterranean-climate regions described above, many of the Mediterranean Basin intermittent streams within the biomonitoring network are not being included in the monitoring programs. An example is the Júcar River Basin in Spain, where part of the biomonitoring network has no biological data available because sampling sites were always dry at the time of sampling [114]. In other cases, such as transboundary Palestinian–Israeli watersheds, the complex political situation restricts the implementation of biomonitoring programs although attempts to adjust biotic indexes have been made [115]. In Chile, biomonitoring programs are not mandatory and are not being fully implemented [116].

Table 2. Examples of studies from Mediterranean rivers analyzing inter-annual variability on selected macroinvertebrate community metrics. CV: coefficient of variability (%) [106] is not included in this table because median and quartiles were reported. Nevertheless, variability was the highest for non-perennial streams examined, similar to results from California.

Study and Region	Period Analyzed	Sampling Sites	Hydrological Regime and Available Stream Characteristics	Community Metrics	CV (%)
[20] California	1977–1983 (6 years)	1	Perennial, spring Stream order = 3	Richness H′	33.2 23.9
		1	Perennial, summer Stream order = 3	Richness H′	22.2 17.9
	1985–2003 (18 years)	1	Non-perennial, spring Stream order = 1	Richness H′	21.3 15.4
		1	Non-perennial, summer Stream order = 1	Richness H′	22.6 25.4
[84] Mediterranean Basin	2002–2003 (1 year)	1	Non-perennial, siliceous	Richness H′	7.6 12.2
[80] California	1984–2003 (20 years)	2	Perennial, spring	Richness EPT IBI	19–26 24–30 24–26
		1	Perennial, summer	Richness EPT IBI	23 51 42
		2	Non-perennial, spring	IBI Richness EPT	22–25 22–29 21–40
[71] Mediterranean Basin	2003–2005 (3 years)	6	Perennial, calcareous Mean stream order = 1.7	Richness H′ EPT IBMWP ICM-11	15.3 18.9 16.8 8.7 24.4
		8	Perennial, siliceous Mean stream order = 1.3	Richness H′ EPT IBMWP ICM-11	7.7 17.5 7.4 7.2 5.6
[81] Mediterranean Basin	1995–2008 (13 years)	1	Perennial, spring calcareous dry	EPT	21.6
		1	Perennial, spring, calcareous wet	EPT	25.2

Even with the above-described limitations and deficiencies, the development of methods for adapting traditional biomonitoring tools to Mediterranean streams and rivers is underway [117,118]. For example, in California, Mazor et al. [118] demonstrated acceptable performance of current biomonitoring indices such as the Southern California Index of Biotic Integrity (IBI) for many intermittent streams. Moreover, innovative approaches, such as one based on terrestrial fauna [119,120] are being developed.

A vital step for the adequate assessment of intermittent Mediterranean rivers is the use of hydrological regime classification as a precondition to performing ecological status assessments [121–123]. In Spain, an ongoing project dedicated to the ecological and hydrological assessment of Mediterranean rivers (i.e., "TRivers" [124]) is developing a tool that allows for an ecologically meaningful classification of a river's hydrological regime, namely as perennial, intermittent-pools, intermittent-dry, and ephemeral/episodic with the possibility of using and comparing different data sources [123]. With this method, current bioassessment methods can be applied in intermittent streams (but not ephemeral streams) during flow conditions by adapting the calendar date for each sampling location according to the period of the year with the highest probability of finding flow conditions. Another important aspect of this tool is determining whether the natural flow regime of a stream has been altered. If this is the case, a "bad" or "poor" hydrological status will be obtained and environmental targets for perennial streams such as the implementation of ecological flows should be applied. A key priority, therefore, is to determine to what extent water quantity may limit the quality of the ecosystem condition in Mediterranean streams. In this sense, hydrological variability, both natural and human-induced, can exacerbate impacts on biotic communities during the dry season under the same level of pressure due to the low or null dilution capacity [11].

A further complication for biomonitoring in Mediterranean rivers is that Larsen et al. [125] found low concordance in the results obtained using macroinvertebrates and fish, recommending that a multi-assemblage approach should be used in biomonitoring. Because fish and macroinvertebrates often show different responses to seasonal and inter-annual variability, long-term data in different Mediterranean-climate regions of the world are needed for effective management of water resources. Likewise, approaches that consider the influence of temporal variability in flow conditions on biotic assemblages and advances in the development of biomonitoring tools in non-perennial stream and river systems are urgently needed. This information would help water managers in Mediterranean-climate regions to provide more robust and accurate methods for distinguishing natural from anthropogenic disturbances.

4.2. Conservation Management in Mediterranean Regions

Streams and rivers from Mediterranean-climate regions show the same trends evident in the global pattern of freshwater-biodiversity loss [126,127] that present alarming declines over the last decades, especially in mollusk and fish populations [128–131]. We suspect that the same is true for many macroinvertebrate species but the data on these taxa at the species level is generally lacking.

The poor conservation status of many species is evidence of a conflict between population growth, land/water use, and maintenance of freshwater biodiversity. The strong seasonal and inter-annual flow variability of Mediterranean systems has led to the extensive development of water storage and most of rivers have been dammed and regulated for water abstraction [9,10]. In addition, most of rivers in Mediterranean regions suffer from pollution and invasive species, among other pressures [10]. Streamflow declines in recent decades have been reported in many Mediterranean regions worldwide [132–134]. For example, in Southwestern Australia, a 50% reduction in discharge over the past 35 years has been observed for some rivers [135]. This trend will continue with predicted climate change and increased water demand [31,132,135,136], and likely will exacerbate current impacts on freshwater biodiversity [79]. Despite numerous efforts in developing environmental policies aiming at protecting freshwater ecosystems and their sustainable use in most of the Mediterranean-climate countries, major challenges persist in implementation [132]. For example, the cyprinid *Anaecipris hispanica*, which inhabits small intermittent streams of the Guadiana River basin, is one of the most threatened species in the Iberian Peninsula, and this population experienced a 50% decline in 10 years despite investments in conservation programs [137].

In this context, testing for the effectiveness of current conservation tools in protecting freshwater biodiversity (e.g., the establishment of protected areas) turns out to be particularly relevant in Mediterranean regions. A recent study in California established a series of priority catchments for native fish conservation, most of them located in Mediterranean-climate regions [138]. The authors assessed the concordance of these catchments with existing protected areas and found that most high-priority catchments were inadequately covered. Likewise, Carrizo et al. [131] identified priority catchments for freshwater conservation at the European scale and showed that most were located in Southern Europe and also not fully covered by existing protected areas. This is not surprising considering that the Mediterranean Basin is, among all the Mediterranean-climate regions of the world, the one with the lowest protection level [128]. At the regional scale, several priority sub-basins were identified in the Guadiana River Basin in the Iberian Peninsula, and similar results regarding low rates of protected-area coverage were found [139]. As a result of the high seasonality and inter-annual variability in flow, the intermittency of many streams, and the inherent variability in populations and communities, the establishment of defensible conservation targets in Mediterranean regions is especially difficult. The conservation of habitat refugia, and the maintenance of connectivity among them, are therefore important aspects to be integrated in the management of these highly variable systems [57]. This has been the approach used in freshwater conservation planning for the prioritization of highly seasonal sub-catchments in Northern Australia [140], and could also be used as a tool for improving conservation management in Mediterranean-climate regions.

The homogenization of flow regimes is particularly deleterious to conservation actions in Mediterranean streams and rivers, and preserving flow variability through the implementation of environmental flows will be critical for their long-term conservation [138,141]. A case study from Putah Creek (California) shows how native fish populations in rivers affected by dams and water abstraction can benefit from environmental flow regimes that integrate streamflow seasonal variability [94]. Before implementation, the fish community was dominated by non-native species downstream across ~30 km of lower Putah Creek. However, the community shifted to one dominated by native fishes across ~20 km of lower Putah Creek after environmental flow releases from the upstream dam included prescribed flow releases in spring as a cue for native fishes to breed and minimum flow releases in summer to maintain surface flow in downstream reaches even during extreme drought [95].

Freshwater biodiversity loss in Mediterranean regions from climate change is expected to be among the highest worldwide [142,143]. Predicted changes include increased variability in natural environmental conditions, with potential negative consequences for species persistence. A 2013 study at the global scale predicted a significant increase in extinction rates for fish with climate change [144], identifying small coastal basins located in the driest areas to be the ones that will experience the highest increase (Figure 5). In the Mediterranean Basin, these correspond to coastal basins from the Region of Murcia in Southeastern Spain, the region of Attica in southern Greece, Cyprus, and most of northern Africa. In South Africa, the West Coast Peninsula will be one of the regions with the highest percent change. The coast of California from Los Angeles to North of Mexico will be the most affected, and a high percent change is also predicted for most of central Chile. However, the study concluded that a few basins will suffer extinctions solely because of climate change, and that anthropogenic threats are by far more relevant in accelerating extinction rates because of habitat loss. Therefore, more information is still needed on how freshwater fauna from Mediterranean regions will respond to global change [79]. However, it is clear that huge efforts for improving water governance by integrating the inherent variability of these systems is urgently needed [132,145–147].

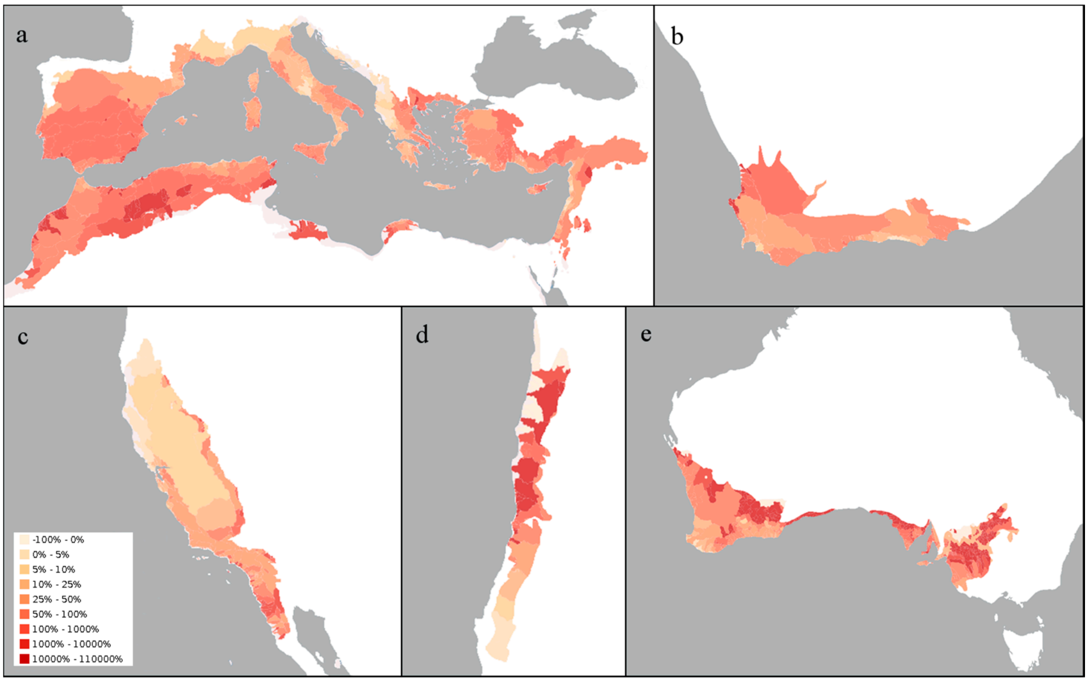

Figure 5. Projected changes (%) in extinction rate of freshwater fish populations between future and current climatic conditions in Mediterranean-climate regions in the world: Mediterranean Basin (**a**); South Africa (**b**); California (**c**); Chile (**d**); and Australia (**e**). Modified from the Global Freshwater Biodiversity Atlas [148].

5. Conclusions

In this article, we have presented numerous examples of how spatial and temporal variability have influenced the assemblages of fish and macroinvertebrates in streams and rivers in Mediterranean-climate regions of the world. This variability results from the highly seasonal rainfall in these areas, and the high degree of variation from year to year. Although the timing of the rainfall and the wet and dry seasons is generally predictable, the year-to-year variation is not.

The annual sequence of flooding and drying requires adaptations and species traits that are often contradictory in terms of surviving these opposing stressors. This has produced a unique fauna in streams and rivers in Mediterranean-climate regions, a fauna that has evolved to respond to these stresses. Under longer or extreme drying events, such as those predicted by climate change scenarios in Mediterranean-climate regions [79,149], the effects of dry years on population and communities will be exacerbated, and the resistance and resilience capacity of Mediterranean river and their biota may be compromised [22]. Under this situation, Mediterranean rivers will experience irreversible "regime shifts", possibly shifting these systems towards undesirable alternative stable states [10,21]. Consequently, tools for managing these systems, such as those related to biomonitoring, climate change, and conservation, must be tailored to the seasonal and inter-annual variability of these systems.

The importance of long-term data sets for understanding interactions among native species and introduced species cannot be overemphasized. These are particularly valuable in understanding the influence of extreme events such as drought (e.g., [21,22]). However, the use of such studies, particularly in regulated systems, for helping guide flow recommendations to benefit native species has only begun, and the value of such an approach is already clear (e.g., [26,94]). Therefore, the preservation of flow variability in Mediterranean rivers and streams will be critical to the long-term conservation of the unique biodiversity found in these systems.

Supplementary Materials: The following are available online at www.mdpi.com/2073-4441/9/1/52/s1, Figure S1: Elevation (m) for the five Mediterranean-climate regions of the world. Data source: SRTM 90 m Digital Elevation Database, v4.1 [28], Figure S2: Mean annual temperatures (1960–1990) for the five Mediterranean-climate regions of the world. Data source: Worldclim Database, v1.4 [29], Figure S3: Mean annual precipitation in mm from 1960 to 1990 for the five Mediterranean-climate regions of the world. Data source: Worldclim Database, v1.4 [29].

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