

CHAPTER 6

General discussion

In chapter 2 of the present thesis it was demonstrated that the vital rates of biphasic life cycles may be aggregated into fertility, growth and looping type. For the sake of clarity by 'looping' it is meant those vital rates that belong to the broad group of survival yet do not represent a somatic growth but rather staying in the same class or even undergo class retrogression. Besides the vital rates, the life strategies may also be aggregated into the fertility (F), growth (G) and looping (L) domains, each dominated by the correspondent type of vital rates, implying these are the most efficient and influential at setting the whole population dynamics. Therefore, in each domain, the most efficient driver for an uneven H:D and its geographical variability is ploidy dissimilarities in the dominant vital rates. Furthermore, it was demonstrated that in the fertility or growth domains the ploidy phase dissimilarities must be huge to promote a conspicuously uneven H:D, whereas in the looping domain subtle ploidy dissimilarities in the looping rates are enough to set a conspicuously uneven H:D. However, having found the most efficient process does not mean it was arrived at the answer. The H:D dynamics is probably more complicated. Experimental evidence by Thornber and Gaines (2004) suggests the global H:D exhibited by a species is indeed given by ploidy phase dissimilarities in fertility rates whereas the spatial variability of the H:D is related to ploidy dissimilarities in the survival rates of the ramets. This hypothesis was tested in chapter 3 yielding predictions of H:D variability that closely matched the H:D patterns observed for the *Mazzaella* genus by Thornber and Gaines (2003). The ploidy dissimilarities in fertility rates are probably related with the differential cytological processes of spore formation, as proposed by Scrosati and DeWreede (1999), Thornber and Gaines (2004) and Fierst et al (2005), whereas the ploidy dissimilarities in survival rates are probably related with the conditional differentiation that Hughes and Otto (1999) found necessary for the evolution and stability of biphasic life cycles. Since ploidy dissimilarities in fecundity and spore performance have often been reported, it is reasonable to question whether these are able to generate the required conditional differentiation. Starting by the spores, the work by Hughes and Otto (1999) was actually presented with the results from conditional differentiation upon the spores, although it

was also tested upon the ramets. The current thesis further demonstrated that if it affects the ability of spores to disperse, differentially between ploidy phases, a spatial niche partition is automatically set at a short spatial scale, that is, at the intra-population level. However, this does not reflect a differential adaptation of the spores to explore a spatial heterogenic environment but it is rather imposed by the own life cycle specificities. A differential adaptation of the spores to explore a spatial heterogenic environment would require a ploidy differential spore settlement performance, which was not tested in this thesis. Regarding ploidy dissimilar fecundity rates, this thesis has proved it to always have a low potential to set an H:D and a spatial niche partition, both at the large and the short spatial scales. On the contrary, This thesis has proved ploidy dissimilarities on the looping rates of the ramets to be efficient at setting an H:D and a spatial niche partition, both at the large and the short spatial scales. Their potential even becomes extraordinary when the life strategy tends to be looping dominated. Only this way it was possible to simulate the conspicuous shift in phase dominance over a very short spatial range as observed for *Gelidium canarense* by Lindgren et al (1998) together with the enormous H:D geographical variability observed for the *Mazzaella* genus by Thornber and Gaines (2004) and for *Chondrus crispus* by many authors and resumed in Garbary et al (2011). Ploidy dissimilarities in the growth rate of the ramets may also have a good potential to generate an H:D and efficient spatial niche partition, provided the life strategy is looping dominated. The dynamics of the growth rates of the ramets was proved to be very dependent on the reproductive output of the populations. When this was high and therefore the life strategy was dominated by fertility, the growth rates of one phase also gave large contributions to the abundance of the opposite ploidy phase. It turned the H:D unpredictable and ploidy dissimilar growth rates a terrible tool for niche partition through conditional differentiation.

The seasonal dynamics of the H:D was not accessed and it was only set the basis for future research on the possibility of a temporal niche partition in chapter 4. Nevertheless, several important preliminary results were obtained. It was determined that ploidy dissimilarities in fertility or growth rates promote the ploidy uneven fast pulse flow of individuals through the life cycle, generating cyclic oscillations of the H:D. This could be a simple and efficient drive for a time niche partition in environments that tend to be stable. However, it may be problematic in seasonal environments because the oscillations are exclusively forced by the life cycle, independent of the seasonal cycle and may even exhibit a shorter wave period than that

of seasonality. If that happens it may pose serious doubts about the viability of ploidy dissimilarities over fertility or growth rates to be the drive for a temporal niche partition. Only looping rates promote a slow diffusive flow of individuals through the life cycle and therefore, only ploidy dissimilarities over looping rates promote a constant and monotonical evolution of the H:D that always points towards the same ploidy dominance as the ploidy looping ratio. Thus, dissimilarities upon looping are the only to guarantee that as the fitness ratio shifts with seasonality the H:D always shifts accordingly for as long as it takes no matter what. Nevertheless, periodic oscillations with a wave period larger than that of seasonality were observed by Thornber and Gaines (2003) in the *Mazzaella* genus, proving that ploidy dissimilarities either over fertility or growth rates are involved, even if combined with ploidy dissimilarities over looping rates to generate a conditional differentiation.

Overall, looping rates, spore survival and a survival dominated life strategy seem to be the best options upon which conditional differentiation may act to generate an efficient niche partition needed for the evolution and stability of isomorphic biphasic life cycles. Nevertheless, future research both on the drives for uneven H:D and on the evolution and stability of isomorphic biphasic life-cycles should evolve to explicitly include the heterogeneity of space and time. The present thesis has demonstrated these interact together to increase significantly the niche partition between ploidy phases.

This thesis gives way to new investigation and new hypothesis to be tested. One field is on the scope of experimental assessment of the currently developed theoretical hypothesis. New field experiments should be designed and put to practice in order to test these new hypothesis and theories. The other one is on the scope of new theoretical modelling for which several objectives are promptly identified: (i) to test the effects of ploidy dissimilar spore settlement, it is expected for it to generate a space and time niche partition; (ii) to test seasonality; (iii) to introduce density dependency in the currently developed models in order to approximate current theory to reality and assess whether competition for resources tends to veil or enhance the expected patterns of H:D behaviour currently postulated. It is an educated guess that competition for resources should enhance the postulated expected patterns of the H:D as, given the presence of dissimilarities between ploidy phases, the best fit should outcast the worst fit; (iv) to introduce the genetic component in the models developed with density dependency as it shall enable to relate the conditions for biphasic life cycles to be evolutionary stable with the H:D patterns expected and observed in the field.