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*Laurea Magistrale in Biologia Evoluzionistica*

**UN APPROCCIO ECO-EVOLUTIVO PER LO STUDIO  
DELLA DINAMICA E DELLA STRUTTURA  
DELLE COMUNITÀ BIOLOGICHE  
IN RISPOSTA ALL'IMPATTO ANTROPICO**

*An eco-evolutionary approach for the study of the dynamics  
and the structure of biological communities in response  
to human-driven global change*

Relatore: Dott. Lorenzo Zane  
*Dipartimento di Biologia*

Co-relatore: Prof. Timothy G. Barraclough  
*Division of Biology, Imperial College London*

***Laureanda:* SILVIA ANTONELLI**

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## **GENERAL BACKGROUND**

### **Global environmental change**

The world and its ecosystems are undergoing rapid global change. The impacts of the main drivers of environmental change – e.g. climatic changes and loss and fragmentation of natural habitats – are predicted to become more important as human exploitation of the environment increases over short time scales (Tylianakis et al., 2008).

Climate change has been widely demonstrated to affect the phenology of species, in particular producing a temporal shift in many spring events, like bud burst, flowering, breaking hibernation, breeding and migrating (Parmesan, 2006). In addition, local changes in species abundances and poleward and upward species range shifts have been documented on all continents and in most of the major oceans both for plant and animal groups (Parmesan, 2006). Human land use has been causing a massive habitat loss for many species belonging to different taxa (Owens & Bennett, 2000; Giam et al. 2010). Furthermore, it enhances biotic invasions and homogenization of biological diversity (Cassey, 2002). Different drivers of environmental change often act in synergy, reducing the overall ability of species to cope with them (Tylianakis et al., 2008).

### **Species interactions and community perspective**

Many studies on environmental change focus on the response of single species, but species are linked with each other through negative (competition, predation, parasitism) and positive (mutualism, facilitation, pollination) interactions, which complicate patterns of single species persistence (Berg et al., 2009). Disruption of community interactions, for example in predator-prey and in plant-pollinator systems, can arise from mismatches in species responses to environmental change – e.g. differences in thermal sensitivity or in dispersal ability (Berg et al., 2009), while new destabilizing interactions, e.g. new pathogens or competitors, can arise from species shift and biological invasions (Tylianakis et al., 2008).

Furthermore, at the community level, environmental factors and species interactions combine to determine the biodiversity of coexisting species: as recognized by Darwin and developed by niche theory, if on the one hand the same environmental filtering selects species with similar ecological characters, on the other hand, species interactions tend to limit the similarity among coexisting species (Cavender-Bares et al., 2009). Community diversity is a key emerging property, as it is expected to be linked to ecosystem-level

functioning, e.g. productivity, nutrient cycling and carbon sequestration, and to resilience to the environmental change (May & McLean, 2007). Diversity, in fact, should enhance complementarity and increase ecosystem function by maximizing resource use, and ensure that sufficient ecological strategies are represented in an assemblage for the persistence of ecosystem function in face of changing conditions (Cavender-Bares et al., 2009).

Therefore, simply scaling up the results of single-species response can be insufficient and the use of a community approach is important to understand how environmental change affects communities (Berg et al., 2009) and ultimately the ecosystem goods and services on which human well-being is dependent (Dobson et al., 2006).

## **Ecological and evolutionary responses to environmental change**

Communities can respond to environmental change through ecological responses, i.e. range or phenological shifts and phenotypic plasticity of traits, but also through evolutionary adaptation (Parmesan, 2006; Kinnison & Hairston JR, 2007). Up to the present, evolutionary and ecological processes have rarely been studied together in multispecies systems (de Mazancourt et al., 2008). However, an emerging synthesis between community ecology and evolutionary biology has been showing that evolutionary processes over short and long time scales can influence community dynamics and patterns; likewise ecological interactions among species within communities can influence micro and macro evolutionary processes (Johnson & Stinchcombe, 2007; Fussmann et al., 2007).

On a short-term time scale, population genetics can help understanding the extent to which human-mediated perturbations enhance contemporary evolution (evolution over humanly observable time-scale) (Kinnison & Hairston JR, 2007), and how evolutionary changes in ecologically relevant traits can influence community dynamics (Johnson & Stinchcombe, 2007). Studies on natural populations have shown that short-term changes in adaptive traits can rescue local populations from extinction (Kinnison & Nelson, 2007). Whether contemporary evolution will be sufficient to mitigate the effects of global change at the species and community levels is however debated (Parmesan, 2006). Rapid evolutionary responses can also carry costs for the species in the long term; for instance through the loss of adaptive genetic diversity (Rodriguez-Trelles & Rodriguez, 1998) or through the selection of trait values that compromise the population growth rates (Rankin & Lopez-Sepulcre, 2005; Orr & Unckless, 2008). In addition, a mismatch among

evolutionary responses of different species due to different rates of evolution can lead to a disruption of species interactions (Berg et al., 2009), for instance in multitrophic networks, e.g. prey-predator and host-pathogen interactions.

On a long time scale, phylogeny makes possible to investigate how much current biodiversity patterns have been influenced by the interplay between evolution and past environmental change. In turn, these studies can help predict what might happen to biodiversity patterns in the face of future changes (Hendry et al., 2010). For instance, phylogeny can help understand how environmental change, in a community context, is able to produce evolutionary changes in the ecological properties of species, and then shape community assembly. Niche conservatism, i.e. the tendency of species and lineages to maintain their ecological niche unchanged over time, has been widely found across different taxa; nevertheless, also niche lability, i.e. the evolutionary radiation of the ecological niche over time, has been documented (Pearman et al., 2007). Recent meta-analyses suggest that ecological processes, e.g. habitat tracking, are the more likely drivers of community composition in relatively saturate systems (Ackerly, 2003). This could be an effect of interspecific competition, that is able to lead to stabilizing selection on species belonging to highly diverse communities, preventing from adaptation of the single species to new environments (de Mazancourt et al., 2008).

Overall, the extent and the conditions under which ecological and evolutionary processes combine, on short and long time scales, in influencing communities dynamics and patterns are still unclear (Johnson & Stinchcombe, 2007), but there is increasing evidence that an integration of community ecology and evolutionary biology would be of a great help in the context of global environmental change (Hendry et al., 2010).

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## **OVERVIEW OF THE THESIS WORK**

The framework delineated above has been investigated in the context of a one-year Master of Research in Ecology, Evolution and Conservation, carried out at Imperial College of London (UK). The work included two months of lectures and two projects of 5 months each.

The lectures regarded the following topics: Plant community ecology and conservation; Speciation and the evolution of biodiversity, Population dynamics and modelling; Demography and management; Global diversity conservation and GIS, Global change ecology and ecosystem function; Statistical computing with R; Advances in modelling population and community ecology with R.

The two projects explored different research areas and different mathematical and statistical approaches for the study of community responses to global environmental change, by integrating ecological and evolutionary aspects. The first project has been carried out at Imperial College and the second at Lausanne University (Switzerland). Each project has been written according to the style of a specific scientific journal (Ecology Letters and Global Ecology and Biogeography respectively).

### **Project 1: modelling eco-evolutionary dynamics of temperature dependent consumer-resource system**

The first project regards the short-time scale interplay between ecological and evolutionary dynamics of communities. The study object is a consumer-resource system; therefore the focus is on interactions between trophic levels. The project investigates the effects of temperature, as environmental variable, on body size, as evolvable trait. The mechanism studied is based on the dependence of metabolic rates – and therefore of the energy flow across the trophic web - on body size and temperature. The approach is based on a mechanistic model of population dynamics (Vasseur & McCann, 2005) based on metabolic theory (Savage et al., 2004), which is integrated with quantitative trait genetics (Iwasa et al., 1991), and investigated by simulations.

## **Project 2: functional and phylogenetic structure of subalpine meadow plant communities**

The second project explores the long-time scale interaction between ecological niche processes and evolutionary processes that shape the structure of communities. The study object is a pool of natural plant communities located in the Swiss Prealps, thus the focus is within trophic levels. The project investigates the role of the main environmental gradient of the area, represented by elevation, in determining the functional and phylogenetic diversity of plant communities. The approach is based on statistical analysis of the functional and phylogenetic structure of the communities, obtained by combining the two complementary methods currently used in literature, respectively based on correlations between different kinds of pairwise species dissimilarities (functional, phylogenetic and niche) and community metrics of functional and phylogenetic diversity (Vamosi et al., 2009, Cavender-Bares et al., 2009).

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# **PROJECT 1: MODELLING ECO-EVOLUTIONARY DYNAMICS OF TEMPERATURE-DEPENDENT CONSUMER-RESOURCE SYSTEM**

## **Abstract**

Species interactions play key role in ecosystem responses to global change. Moreover, global change exerts a selective force on traits involved in ecological interactions, potentially causing contemporary evolution and feedback effects on ecological dynamics. Therefore, responses to warming of a consumer-resource system are investigated with an eco-evolutionary approach.

A mechanistic framework based on body size and temperature dependence of physiological rates is adopted. Evolution of body size is incorporated through quantitative genetic equations.

The model shows that metabolic selective forces drive body size into co-evolutionary arms races. Evolution is more pronounced if species' background specialisation is weak and consumption specialisation is strong. Warming affects the evolutionary dynamics amplifying changes in species' body sizes. Finally, evolution of body sizes can either prevent shift from equilibrium dynamics to cycles, or enhance consumer extinction in response to warming, depending on temperature dependence of consumer physiological rates.

## Introduction

Studying the dynamics of interactions between species is key to understanding the responses of communities and ecosystems to global environmental change. Some studies, in fact, show that the effects of the relative mismatch between species responses can be as or more relevant than the single species responses in determining species persistence and ecosystem function (Berg et al. 2009).

Recent studies suggest that evolution can occur in ecological time, with relevant feedbacks between ecological and evolutionary dynamics (Johnson & Stinchcombe 2007, Fussmann et al. 2007). Global change exerts a selective pressure on many traits involved in ecological interactions. As a consequence, contemporaneous evolution of those traits can indirectly affect the ecological dynamic of the system. Therefore, combining ecological and evolutionary dynamics can improve the understanding of community responses to global change.

The consumer-resource interaction is a suitable framework to address the problem of how species differences affect community responses to global change. The consumer-resource system is widely studied as a basic motif of ecosystem food webs, and, potentially, a consumer-resource model can be extended easily to multi-species assemblages (Williams, 2005).

In order to investigate consumption interactions under global change, a general energetic framework is adopted (Iodzis & Innes, 1992; Vasseur & McCann, 2005). According to metabolic ecology, the flow of energy through the food web can be described in a general way by looking at two main components: body size and temperature (Gillooly et al. 2001, Savage et al. 2004). These two factors are suggested to be the major determinants of the physiological rates of all organisms, according to simple mathematical relationships. Body size dependence of rates is widely modelled as a power law function:  $y = \alpha m^\beta$ , with the exponent  $\beta$  equal to  $-1/4$  for all organisms, and the coefficient  $\alpha$  varying according to broad metabolic categories (Yodzis & Innes, 1992). Even though the "true" value of the exponent is still controversial, allometric relationships are supported by empirical evidence (Yodzis & Innes, 1992) and are recently derived from transport network first principles (Banavar et al. 1999, Brown et al. 2004). Temperature dependence is derived from enzyme kinetics principles (Gillooly et al. 2001), and it is modelled as an exponential function:  $y = e^{-E/kT}$ , where  $T$  is temperature in Kelvin,  $E$  is the activation energy of the physiological process and  $k$  is the Boltzmann's constant. Moreover, body size seems to be a key determinant of the strength of consumption interactions. Some studies in fact suggest that consumers

preferentially feed on resources according to an optimal log-body size ratio (Brose et al. 2006).

Therefore, such a metabolic framework offers a powerful tool to investigate the qualitative dynamic of a general consumer-resource system. More important, from an evolutionary point of view, it allows focus on temperature as a specific environmental selective factor and on body size as a relevant evolvable trait, which can change and affect the ecological dynamics in a mechanistic way.

There is good empirical evidence that both body size and temperature dependence of physiological rates could play a key role in responses to global change. Thermal sensitivity difference among physiological rates seems one of the most important factors that determines mismatches into trophic interactions and then affects species persistence and food web functioning (Berg et al. 2010). Regarding body size, there is evidence that a general shift of trophic webs to smaller dimensions could be a consistent consequence of global warming (Daufresne et al. 2009).

A quantitative trait genetic approach (Iwasa et al. 1991) is used to track the evolution of species' body sizes. It allows the avoidance of any separation between ecological and evolutionary time, and so more realistic investigation of the eco-evolutionary feedbacks (Taper & Case 1992, Abrams 2001). A weak selection assumption is made in order to keep the model simple (Iwasa et al. 1991) and a stabilising background selection function is added (Lande, 1976) in order to avoid the evolutionary system to reach unrealistic body sizes.

The study is aimed at assessing whether body size evolution in the context of the energetic consumer-resource framework can significantly affect the system under temperature increase. Firstly, the study investigates the evolutionary dynamics produced by metabolic selective forces, and the conditions under which body size evolution is relevant. Then, the effects of warming on evolution of body sizes are analysed. Finally, some insights are given about how evolution can affect the ecological system, and in particular, the stability of population dynamics. Strengths and weaknesses of the eco-evolutionary framework adopted are highlighted for further developments.



## Materials and methods

The derivation of the model is described in full in the appendix A, but key features are as follows.

The ecological model is based on a Lotka-Volterra model, improved with a logistic growth of the resource and a generalized type III functional response, which are demonstrated to be important features for the stability of the dynamic.

The physiological rates are parameterized respect to body size (Yodzis & Innes, 1992) and temperature (Vasseur & McCann, 2005), according to recent advances of metabolic ecology (Gillooly et al. 2001). This approach allows defining a general mechanistic framework constrained in a realistic way.

The model is expressed in individual density instead of biomass density, in order to incorporate evolution. Specifically, the conversion is needed both to have an expression for individual fitness, and to have a variable independent on body size, in order to make ecological equations valid even under body size change.

The strength of consumer-resource interaction (consumer preference) is modelled as a function of the body size ratio of the two species (Lewis & Law, 2007). This explication is essential in a context of changing body sizes. In fact, the ability of the consumer to feed on the resource can be affected by body size evolution, and, vice versa, can produce a selective force on body sizes.

Equations are also converted in  $\log_{10}$  of body size, in order to deal with body size skewed distributions. Firstly, this allows tracking the evolution of the arithmetic mean of the log-body size, that is a more correct measure of the central tendency for skew distributions, than the arithmetic mean of body size. Secondly, it allows considering the variance parameters (which appear in consumer preference, stabilising selection and quantitative genetic equation) independent on the mean, so constant in time and - in the simplest hypothesis - equal for the two species.

Body size evolution is modelled by quantitative genetic equations, under the simplifying condition of weak selection (the variance of the trait is assumed small compared to the variance of the fitness function) (Iwasa et al. 1991). This approach has the advantage to allow no separation between ecological and evolutionary time and to be not invalidate by frequency-dependent fitness. At the same time, it is computationally easy, as it does not require calculating integrals over the bulk of body size distribution and explicating the effects of the interaction between each individual body size with all the others.

Stabilising selection around an optimal body size (Lande, 1976) is added to species growth rates, in order to prevent body sizes to evolve to unrealistic values.

Finally, the equations are normalized respect to the maximal growth rate of the resource

at its optimal body size and at standard temperature, in order to define a timescale suitable for systems set at every order of magnitude.

The model equations are the followings:

$$\frac{dN_i}{dt'} = r'_{i\ tot}(\bar{M}_i)N_i \quad [1]$$

$$\frac{d\bar{M}_i}{dt'} = V_{ai} \left. \frac{\partial r'_{i\ tot}(M_i)}{\partial M_i} \right|_{M_i = \bar{M}_i} \quad [2]$$

The variables of the model are the individual densities of the resource ( $N_1$ ) and the consumer ( $N_2$ ) ( $n\ m^{-3}$ ), and the mean log10-body size of the resource ( $M_1$ ) and the consumer ( $M_2$ ) ( $\log_{10}(Kg)$ ). The parameter  $V_{ai}$  is the genetic additive variance of the species  $i$  ( $\log_{10}(Kg^2)$ ).

The model is built around the individual normalized per capita growth rates of the species,  $r'_{i\ tot}(M_i)$ , which determine both the ecological and the evolutionary dynamics. They are defined as a sum of three components: intrinsic growth or loss ( $R$ ), consumption ( $J$ ) and stabilising selection ( $S$ ):

$$r'_{1\ tot}(M_1) = \frac{R_{n\ max} \hat{R}_n - J_{n\ max} \hat{J}_n N_2 - S_1}{R_{n\ max}(M_0, T_0)} \quad [3]$$

$$r'_{2\ tot}(M_2) = \frac{-D_n + c_n J_{n\ max} \hat{J}_n N_1 - S_2}{R_{n\ max}(M_0, T_0)} \quad [4]$$

The resource intrinsic growth rate is the product of  $R_{n\ max}$ , the maximum intrinsic growth rate, and  $\hat{R}_n$ , the normalized growth. Similarly, the consumption rate is the product of  $J_{n\ max}$ , the maximum ingestion rate, and  $\hat{J}_n$ , the normalized functional response, per resource individual. The intrinsic loss rate of the consumer is  $D_n$ .  $c_n$  is the conversion efficiency of resource individual in consumer individual. Finally,  $S_1$  and  $S_2$  are the stabilising selection functions on the resource and the consumer.

The physiological rates are modelled as a function of body size and temperature, according to metabolic allometric relationships (power laws) and the Boltzmann factor (exponential function):

$$R_{n_{\max}} = f_r a_r(T_0) 10^{-\frac{1}{4}M_1} e^{E_r(T-T_0)/kTT_0} \quad [5]$$

$$c_n J_{n_{\max}} = f_j a_j(T_0) 10^{-\frac{1}{4}M_2} e^{E_j(T-T_0)/kTT_0} \quad [6]$$

$$D_n = a_d(T_0) 10^{-\frac{1}{4}M_2} e^{E_d(T-T_0)/kTT_0} \quad [7]$$

The allometric coefficients  $a_r(T_0)$ ,  $a_j(T_0)$  and  $a_d(T_0)$  ( $\text{Kg Kg}^{-1} \text{year}^{-1} \text{Kg}^{\frac{1}{4}}$ ) express the dependence of each rate on body size, at the standard temperature  $T_0=293$  K.  $f_r$  and  $f_j$  (non-dimensional) are the realized fractions of  $a_r(T_0)$  and  $a_j(T_0)$  due to ecological limitations to the physiological rates.

The activation energies,  $E_r$ ,  $E_j$  and  $E_d$  (eV) express the dependence of each rate on temperature.  $T$  is the environmental temperature (K) and  $k$  is the Boltzmann constant (eV/K).

The normalized intrinsic growth and functional response take account of the resource density-dependence effects, respectively in resource growth and consumption:

$$\widehat{R}_n = 1 - \frac{N_1}{K_n} \quad [8]$$

$$\widehat{J}_n = \frac{z N_1^q}{z N_1^q + N_0^q} \frac{1}{N_1} \quad [9]$$

Regarding intrinsic growth,  $K_n = \frac{K}{10^{M_1}}$  [10] is the resource carrying capacity in individual density, where  $K$  is the resource carrying capacity in biomass density ( $\text{Kg m}^{-3}$ ).

Regarding consumption,  $N_0 = \frac{B_0}{10^{M_i}}$  [11] is the half-saturation individual density (resource individual density needed to reach half-saturation of consumer), where  $B_0$  is the half-saturation biomass density ( $\text{Kg m}^{-3}$ ).  $q$  is the control parameter in functional response (if 1 it gives a type II functional response, if 2 a type III) (non-dimensional).

Consumer preference  $z$  (Gaussian function) is incorporated in the normalized functional response as a factor of the attack rate. Consumer preference can be considered as a measure of the effective proportion of the resource population that a consumer can actually eat, because of a suitable body size:

$$z = e^{\left[ -\frac{(a-(M_2-M_1))^2}{2b^2} \right]} \quad [12]$$

$a$  (non-dimensional) is the optimal consumer-resource log-body size difference and  $b$  (non-dimensional) is the standard deviation of consumer preference.

Consumption interaction involves an individual conversion efficiency factor:  $c_n = c \frac{10^{M_1}}{10^{M_2}}$  [13], where  $c$  is the conversion efficiency of resource biomass to consumer biomass (non-dimensional).

Finally, the stabilising selection functions (quadratic functions) are defined as follows:

$$S_1 = \frac{(Mo_1 - M_1)^2}{2v_1^2} \quad [14]$$

$$S_2 = \frac{(Mo_2 - M_2)^2}{2v_2^2} \quad [15]$$

$Mo_1$  and  $Mo_2$  are the optimal log-body size for the resource and the consumer, while  $v_1$  and  $v_2$  are the standard deviations of resource and consumer stabilising selections ( $\log_{10}(Kg)$ ).

Timescale normalisation is obtained by dividing the consumer and resource total per capita growth rates by the resource intrinsic maximum growth rate at its optimal body size and standard temperature:

$$R_{n_{\max}}(Mo, To) = f_r a_r(To) 10^{-\frac{1}{4}Mo_1} \quad [16]$$

Thus, the explicit expressions of growth rates are:

$$r'_{1tot}(M_1) = \left( \begin{array}{l} f_r a_r(T_0) e^{E_r(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_1} \left(1 - \frac{N_1}{K}\right) + \\ \frac{10^{M_1}}{c \frac{10^{M_2}}{10^{M_1}}} \frac{\left(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1\right)^q}{\left(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1\right)^q + \left(\frac{Bo}{10^{M_1}}\right)^q} \frac{N_2}{N_1} + \frac{1}{a_r(T_0) 10^{-\frac{1}{4}M_{O_1}}} \\ - \frac{(M_{O_1} - M_1)^2}{2v_1^2} \end{array} \right) \quad [17]$$

$$r'_{2tot}(M_2) = \left( \begin{array}{l} -a_d(T_0) e^{E_d(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} + \\ + f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} \frac{\left(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1\right)^q}{\left(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1\right)^q + \left(\frac{Bo}{10^{M_1}}\right)^q} + \frac{1}{a_r(T_0) 10^{-\frac{1}{4}M_{O_1}}} \\ - \frac{(M_{O_2} - M_2)^2}{2v_2^2} \end{array} \right) \quad [18]$$

The analytical tractability of the model is prohibitive, but the model can be reduced to Vasseur and McCann's (2005) model if consumer preference is equal to 1 ( $a = M_2 - M_1$ ), stabilising selection penalization is equal to 0 ( $M_i = M_{O_i}$ ), the functional response is type II ( $q = 1$ ) and, most importantly, evolution is forbidden ( $V_{a_i} = 0$  or alternatively  $v_i \rightarrow 0$ ).

This equivalence provides a guide-line for parameter space investigation, performed by numerical simulations, and allows direct comparison of outcomes of the eco-evolutionary model and the pure ecological model of Vasseur and McCann (2005).

The parameters (Table. 1) are constrained into a realistic range by looking at empirical estimates when available; alternatively, a broader range of variability is discussed. Simulations are performed for a phytoplankton-zooplankton system, by using Vasseur and McCann (2005) parameter values. Regarding initial conditions, equilibrium points are locally stables, but the system is quite sensitive to changes in the initial body sizes. Simulations are performed by setting, for simplicity, initial body size values,  $M_1$  and  $M_2$ , equal to the optimal species body sizes,  $M_{O_1}$  and  $M_{O_2}$ .

Simulations are performed with R 2.10.1 (R Development Core Team 2010).

## Results

The study firstly explores the main kinds of evolutionary dynamics produced by metabolic selective forces (Fig. 1).

The system displays decreasing arms races (Fig. 1a) in the simplest case in which the optimal log-body size difference for consumption is equal to the difference of optimal log-body sizes ( $a = Mo_2 - Mo_1$ ) and the stabilising selection variance is equal in the two species ( $v_1 = v_2$ ). The resource body size decreases, and the consumer tracks it, until both of them reach an equilibrium point.

Increasing arms races (Fig. 1b) can occur when the optimal body size ratio for consumption is great enough with respect to the ratio between species' optimal body sizes.

Moreover, if the stabilising selection variance of the consumer is great enough with respect to the resource variance, arms races can repetitively change direction leading to stable co-evolutionary cycles around the optimal body sizes (Fig. 1c).

A qualitative analysis of the drivers of the dynamics is obtained by looking at fitness landscapes (Fig. 1), which represent the per capita growth rates of each species as a function of the respective body sizes. The slope of the per capita growth rate function, in correspondence of the current body size, determines the instantaneous direction and speed of the evolution of each species body size, according to the equation [2] (if the slope is positive, body size increases, if negative, it decreases).

Three additive components co-occur in determining fitness landscape: intrinsic growth (or loss), consumption and stabilising selection. The stabilising selection function is a symmetric function with its maximum correspondent to the optimal background body size of each species,  $Mo_i$ . The intrinsic growth (or loss) is a monotone function; it is strongly higher for small resource body sizes, while it is weakly higher for consumer big body sizes. The consumption function is a curve with a minimum for the resource, and a maximum for the consumer. Both of them shift in relation to changes of the other species' body size. If a decreasing arms race occurs,  $a \leq Mo_2 - Mo_1$  (Fig. 1a), smaller body sizes in both the species display a higher rate due to consumption, while, if an increasing arms race occurs,  $a > Mo_2 - Mo_1$  (Fig. 1b), bigger body sizes in both the species have a higher rate. Finally, if there are cycles, for  $v_2 = v_1$  (Fig. 1c), both the patterns are present, alternate in time.

The conditions under which evolution of body sizes is relevant are investigated.

The extent and the intensity of evolutionary changes, whatever they are (body size

increase, decrease or oscillation) depend strongly on two parameters: standard deviation of stabilising selection,  $\nu$ , and the standard deviation of consumer preference,  $b$ .

Decreasing arms races (Fig. 2) are a representative example.

Fitness landscapes show that the strength of the stabilising force decreases by increasing  $\nu$  (this makes the curve flatter), while the strength of consumption selective force increases by increasing  $b$  (this makes the curve steeper).

Temporal dynamics show that, when the stabilising selection is weak (low values of  $\nu$ ) and the consumer preference is strong (high values of  $b$ ), the system displays a bigger change in body sizes and a faster dynamic. Specifically, stabilising selection mainly affects the amount of departure from optimal body sizes (Fig. 2a, 2b versus 2c, 2d). Consumer preference, instead, mainly affects the speed of the evolutionary change (Fig. 2a, 2c versus 2b, 2d).

After the investigation of evolutionary trends in absence of temperature change, the study concentrates on temperature effects of the eco-evolutionary dynamics.

Firstly, the effects of warming on body size evolution are analyzed (Fig. 3). Simulations suggest that, despite the different dynamics (decreasing (a), increasing (b) or cycling (c) body sizes), warming produces an increase of the extent and the speed of body size change. Fitness landscapes show that the steepness of intrinsic growth and consumption functions increases with temperature.

Secondly, the study investigates some feedbacks of body size evolution to the ecological responses to warming (Fig. 4). The analysis explores two different sets of ecological conditions, which are expected to be destabilized by warming according to Vasseur and McCann's (2005) analysis. Eco-evolutionary dynamics are compared to pure ecological dynamics, at different temperatures, in order to assess whether evolution prevents from population dynamics destabilisation in response to warming, or enhances it.

Simulations show a different effect in the two cases analysed. The first case (a) regards high-enriched systems ( $K$  high) with a positive consumer thermal impact ( $E_j - E_d > 0$ ).

In these conditions, evolution increases the stability of the system, preventing it from shifting into cycles, as temperature increases. On the contrary, in the second case (b) (low-enriched systems with a negative consumer thermal impact) evolution decreases the stability of the system, enhancing consumer extinction with warming.

## Discussion

The analysis of the model suggests that body size evolution, due to temperature-dependent metabolic interactions, can produce relevant effects on the responses of the consumer-resource system to increasing temperature.

The energetic framework generally drives body size to evolve according to arms races, where the consumer tracks the resource change. There is evidence that either increasing or decreasing arms races, or co-evolutionary cycles can occur.

Fitness landscape analysis gives some insights about the main metabolic selective forces acting on body sizes. Stabilising selection is a conservative force that keeps body sizes near to their optimum, contrasting any evolutionary change. Intrinsic growth or loss is a directional force that strongly selects for resource small body sizes (faster growth rates), and weakly selects for consumer big body sizes (slower loss rates). The difference in strength of selection between resource and consumer is, for a great part, due to the fact that the slope of the allometric relationships (power laws) is more accentuated if body size is small. This suggests that, in a multispecies system that spans many orders of magnitude, body size can play an important role in determining the strength of metabolic selection at different trophic levels.

Consumption selection is the most interesting force, as it links the evolutionary dynamics of the two species. Consumption implicitly assumes that there is a "conflict of interests" between resource and consumer. If one species' fitness is maximized, the other is minimized. Thus, consumption makes the resource escape from the consumer and the consumer track the resource evolution, leading to arms races. The direction to evolution given by consumption alone depends on the relationship between the optimal body size ratio and the species optimal body sizes. If smaller consumers eat bigger resources ( $a < Mo_2 - Mo_1$ ), smaller body sizes in both the species are advantaged, and both species' body size decreases. If bigger consumers eat smaller resources ( $a > Mo_2 - Mo_1$ ), bigger body sizes in both the species are advantaged, and both species' body size increases. The likelihood of the different options should be assessed, but there is some suggestion that the second option is more frequent than the first in real systems, leading to the prediction that consumption interaction alone generally selects for bigger body sizes. Interestingly, the direction given by consumption interaction to body size evolution does not depend only on consumption itself. If other strong directional forces act on the system, and optimal body size for predation is near to the species' body size ratio (consumption is quite neutral respect to small or big body sizes), consumption interaction can enhance the directional change that is already happening,



whatever it is.

Considering the balance between the different metabolic selective forces, the relative likelihood of decreasing and increasing arms races is uncertain, but simulations suggest that the strength of intrinsic growth selection for small body sizes is quite strong compared to consumption advantage of big body sizes, and could often predominate leading to decreasing arms races.

The extent and the intensity of arms races depend on the strength of stabilising selection (lower of higher values of  $\nu$ ) and of consumer preference (higher for lower values of  $b$ ). When background specialisation is weak, the system is more allowed to evolve, and body sizes departure from their optimal is higher. When consumption specialisation is strong, the co-evolutionary dynamic is faster. Thus, the conditions under which evolution is expected to be significant are both a weak background specialisation and a strong consumption specialisation. One interesting point to be deepened regards the relative strength of stabilising selection in the consumer respect to the resource. In fact, if the consumer is weakly constrained respect to the resource, arms races can repetitively change direction leading to stable co-evolutionary cycles.

The most important evolutionary response to temperature is an increase of the extent and the speed of body size change. According to fitness landscape analysis, this effect is mainly due to the fact that the selective directional pressures, due to intrinsic growth and consumption, increase with temperature. In fact, physiological rates are proportionally increased with warming, according to the exponential Boltzmann factor, so body sizes that display higher rates are subjected to a greater absolute increase of their rates.

Evolution of body sizes also produces significant feedbacks to the ecological dynamics.

The first evident general pattern that emerges from simulations is an effect of evolution on the stability of the population dynamics.

According to Vasseur and McCann's (2005) analysis, the ecological dynamic without evolutionary input can be subjected to two kinds of destabilization, depending on the consumer thermal impact ( $CTI = E_j - E_d$ ). If the consumption rate of the consumer increases with warming more than the loss rate ( $E_j > E_d$ , so  $CTI > 0$ ), high-enriched (high  $K/Bo$ ) stable equilibrium systems can be driven to stable limit cycles, leading eventually to extinction because of demographic stochasticity and genetic depression. In the opposite case ( $E_j < E_d$ , so  $CTI < 0$ ), warming could drive low-enriched stable equilibrium systems to mathematical extinction of the consumer. Vasseur and McCann (2005) suggest that the first situation is the most likely to occur, but the likelihood of the

two situations is uncertain because of the lack and the high variability of empirical data for  $E_j$  and  $E_d$ . Interestingly, the eco-evolutionary model shows that in the first case (high-enriched systems with  $CTI > 0$ ) evolution increases the stability of the system, preventing it from shifting into cycles as temperature increases. On the contrary, in the second case (low-enriched systems with  $CTI < 0$ ) evolution decreases the stability of the system, enhancing consumer extinction with warming.

This suggests that evolutionary responses to global warming could generally prevent the destabilization of ecological systems, but could in some cases produce maladaptations enhancing ecological destabilization.

In general, the study can provide some suggestions for building up eco-evolutionary models to study community responses to warming.

The main strength of the model is to investigate a mechanistic and general energetic consumer-resource framework, concentrating on two key elements - temperature (selective force) and body size (evolvable trait) - which are expected to strongly affect the system dynamic. Another key element is the absence of any separation between ecological and evolutionary time, obtained by a quantitative genetic approach. Other features that can improve the model are also explored: consumer preference dependent on body size ratio, conversion in individual densities and in log of body sizes, stabilising selection and timescale normalisation.

Limitations of the model, due to simplifying assumptions, and relative open questions are discussed below. From an ecological perspective, the model is suitable for species that are characterized by relative low body size variability, which makes possible to consider the individual rate of the mean body size as a good measure of the population growth rate. Also, according to the inclusion of the Boltzmann factor, the model is valid within a limited temperature change, below the critical threshold at which physiological processes rapidly decrease. The model is more appropriate for those organisms whose rates strongly depend on environmental temperature, because of lack of behavioural or metabolic thermoregulation. Anyway, it can be extended to others metabolic groups by properly defining the actual activation energy parameters (for example, for endotherms, they could be set equal to 0 according to a first approximation). Moreover, the simulations are performed for  $f_r$  and  $f_j$  equal to 1, which means that resource intrinsic growth and consumption are assumed to be just physiologically and not ecologically limited processes (Vasseur and McCann, 2005). Further investigation is needed for different metabolic types and different ecological limitation extent, but there is evidence that the qualitative dynamic should be similar, even though with a different probability to undergo the qualitative predictions of the model (Vasseur and McCann, 2005).

The allometric coefficients for biomass density are used in absence of more detailed information on the individual density coefficients, thanks to the assumption that fully-grown individuals compose populations. In any case, eventual differences in allometric coefficients should not affect the qualitative dynamics, similarly as above.

To be noticed, the ecological model relies also on the assumption of some key parameters to be independent on body size and temperature (carrying capacity  $K$ , biomass half saturation density  $B_0$ , conversion efficiency  $c$ ), whose discussion is covered in Vasseur and McCann (2005).

A type II functional response is used in the simulations in order to make possible comparisons with Vasseur and McCann (2005) model, but a type III functional response could be performed, in order to allow release of consumption pressure when the resource is rare (which could be important for the stability of multispecies systems).

Finally, predation preference is a key feature in the model. Especially in a multispecies system, it could be made more realistic by including a trade-off between consumer generalism and capture ability (Lewis & Law, 2007). The optimal ratio for predation plays an important role, because it can produce increasing or decreasing arms races. A further investigation could be done to understand if it is generally smaller, equal or bigger respect to the ratio between species body sizes.

The most relevant assumptions regard the evolutionary aspects of the model.

Phenotypic plasticity and evolution of other traits (i.e. thermal sensitivity), in response to warming, are neglected, as an investigation on their relative importance is out of the aims of this study.

The model is valid under the condition of weak selection: the variance of body size is assumed to be relatively low respect to the variance of the growth rate within the populations. A non-simplified quantitative genetic approach (Taper & Case, 1992) would require calculating integrals over the bulk of body size distribution and explicating the effect of the interaction between each individual body size with all the others, therefore the simplified approach (Iwasa et al. 1991) has been chosen for the sake of model simplicity.

Another fundamental assumption of the model regards stabilising selection.

The energetic consumer-resource framework alone drives species body sizes to unrealistic values, towards arms races, suggesting that other relevant selective pressures should be considered. Thus, metabolic fitness function is multiplied by a stabilising factor (Lande, 1976), making metabolic fitness decrease proportionally according to the departure from an optimal body size. This is a simple and generally used way to take account of all the background stabilising forces that influence species body size, without the need to make explicit assumptions about them.

Two considerations have to be made about this assumption: firstly, it makes it necessary to set a theoretical optimal species body size based only on non-metabolic forces, and so which is prohibitively difficult to quantify in real systems. Secondly, it produces the effect that smaller body sizes and high temperature systems are relatively less constrained, because physiological rates increase with body size and temperature, while stabilising selection remains unchanged. The model is quite sensitive to this assumption.

Regarding body size, if the system is composed of species of very different body size, the strength of stabilising selection can be very different, relatively to their respective physiological rates, the bigger species being disproportionately constrained. If the strength of stabilising selection is adjusted (by changing the standard deviation value  $v$ ), in order to make it of the same order of magnitude of each species rates, the systems can shift from equilibrium dynamic to cycles. Independence of stabilising selection on rates might produce also an effect on the probability of extinction of bigger body sizes, because they would be additionally limited in their ability to track the evolution of resources.

Regarding temperature, stabilising selection assumption is key because the increase in body size change due to warming is mainly caused by the relative increase of metabolic selective forces respect to stabilising selection (that remains unchanged).

Further study is needed to deepen this issue. For example, it could be possible to explore the effects of adding stabilising selection in a more mechanistic way, by directly constraining the rates.

In synthesis, the work represents only a preliminary investigation on modelling eco-evolutionary dynamics of communities subjected to global change. However, it allows definition of some general predictions. Metabolic interactions drive body sizes into evolutionary arms races, which are more pronounced if background specialization of species is weak and consumption specialization is strong. Warming increases evolutionary change of body sizes. Finally, body size evolution can have either a stabilising or destabilising effects on population dynamics, depending on temperature dependence of consumer physiological rates. At the same time, the work highlights some key methodological strengths and weaknesses that could be taken into account in further developments.

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## Figures and tables

**Table 1.** Parameter values used in the simulations. Extensive definition of the parameters is in the main text. \* Values from Vasseur & McCann (2005)

**Figure 1.** Main types of evolutionary dynamics: decreasing arms races (a), increasing arms races (b), cycles (c), no evolution (d).

Temporal dynamics of population densities and body sizes of the two species are shown respectively in the first and second columns. Resource=black, consumer=red.

Fitness landscape (per capita growth rate plotted against body size) of resource and consumer are displayed in the third and fourth columns. Intrinsic growth or loss=red, consumption=green, stabilising selection=blue, total rate=black, vertical line=actual body size, horizontal line=actual total growth rate, slope of the tangent proportional to the actual rate of change of body size.

Simulations are performed at  $T = T_0$ ,  $K=0.9$ ,  $b=0.1$ ,  $v_1=0.03$ ,  $v_2=0.03$  (a,b) or 0.05 (c),

$a=4.22$  (a,c,d) or 4.4 (b),  $V_{a1} = V_{a2}=0.0001$  (a,b,c) or 0 (d).

Fitness landscapes are made at time=200, except the last one in (c) (time=4000).

**Figure 2.** Effects of stabilising selection and consumer preference strengths on evolutionary dynamics, and respective fitness landscapes. From top to bottom, decreasing strength of stabilising selection:  $v_1 = v_2=0.02$  (a,b) or 0.03 (c,d). From left to right: increasing strength of consumer preference:  $b=0.3$  (a,c) or 0.1 (b,d). Simulations are performed at  $T = T_0$ ,  $K=0.9$ ,  $a=4.22$ ,  $V_{a1} = V_{a2}=0.0001$ . Fitness landscape is made at time=200.

**Figure 3.** Effects of warming on three different dynamics: decreasing arms races (a1, a2), increasing arms races (b1, b2) and cycles (c1, c2), and respective fitness landscapes.  $T=293$  in the left side (a1, b1, c1),  $T=300$  in the second two columns (a2, b2, c2). Simulations are performed at  $K=0.9$ ,  $b=0.1$ ,  $v_1=0.03$ ,  $v_2=0.03$  (a, b) or 0.05 (c),  $a=4.22$  (a, c) or 4.4 (b),  $V_{a1} = V_{a2}=0.0001$ ,  $E_j=0.772$ . Fitness landscape is made at time=200.

**Figure 4.** Effects of evolutionary change on population dynamic stability under temperature increase. Two cases are analyzed:  $CTI>0$  ( $E_j=0.772$ ) and high enriched system ( $K=1.1$ ) (a), and  $CTI<0$  ( $E_j=0.462$ ) and low enriched system ( $K=0.5$ ) (b). In

each case temporal dynamics are performed at standard temperature ( $T=293$ ) (left side:  $a_1, a_3, b_1, b_3$ ) and high temperature ( $T=300$ ) (right side:  $a_2, a_4, b_2, b_4$ ), without evolution ( $V_{a_1} = V_{a_2} = 0$ ) (top:  $a_1, a_2, b_1, b_2$ ) and with evolution ( $V_{a_1} = V_{a_2} = 0.0004$ ) (down:  $a_3, a_4, b_3, b_4$ ). Other parameters are:  $a=4.22, b=0.1$  and  $v_1 = v_2 = 0.03$ .

| Parameter  | Units  | Values                 | Comments   |
|------------|--|------------------------|--|
| $B_0$      | $\text{Kg m}^{-3}$                                     | 1                      |  |
| $K$        | $\text{Kg m}^{-3}$                                     | variable (0.5-1.1)     | Importance of the ratio $B_0/K$ (Yodzis & Innes, 1992) |
| $q$        | -  | 1                      | Functional response type II*                           |
| $a_r(T_0)$ | $\text{Kg Kg}^{-1} \text{ year}^{-1} \text{ Kg}^{1/4}$ | 0.386                  | Phytoplankton*   |
| $a_j(T_0)$ | $\text{Kg Kg}^{-1} \text{ year}^{-1} \text{ Kg}^{1/4}$ | 9.7                    | Invertebrates*   |
| $a_d(T_0)$ | $\text{Kg Kg}^{-1} \text{ year}^{-1} \text{ Kg}^{1/4}$ | 0.51                   | Invertebrates*   |
| $f_r$      | -  | 1                      | Physiological limitation*                              |
| $f_j$      | -  | 1                      | Physiological limitation*                              |
| $c$        | -  | 0.45                   | Herbivores*  |
| $E_r$      | eV   | 0.467                  | Phytoplankton*   |
| $E_j$      | eV   | Variable (0.772-0.462) | Invertebrates*   |
| $E_d$      | eV   | 0.652                  | Invertebrates*   |
| $k$        | eV   | 8.618 e-5              |  |
| $T_0$      | K  | 293                    |  |
| $T$        | K  | variable (293-300)     |  |
| $a$        | -  | variable (4.22-4.4)    | Phytoplankton and zooplankton system*                  |
| $b$        | -  | variable (0.1-0.3)     |  |
| $V_{a_1}$  | $\log_{10}(\text{Kg}^2)$                               | variable (0.0001-0)    |  |
| $V_{a_2}$  | $\log_{10}(\text{Kg}^2)$                               | 0.0001                 |  |
| $Mo_1$     | $\log_{10}(\text{Kg})$                                 | -11.22                 | Phytoplankton*   |
| $Mo_2$     | $\log_{10}(\text{Kg})$                                 | -7                     | Zooplankton*   |
| $v_1$      | $\log_{10}(\text{Kg})$                                 | variable (0.02-0.3)    |  |
| $v_2$      | $\log_{10}(\text{Kg})$                                 | variable (0.02-0.05)   |  |

**Table 1**



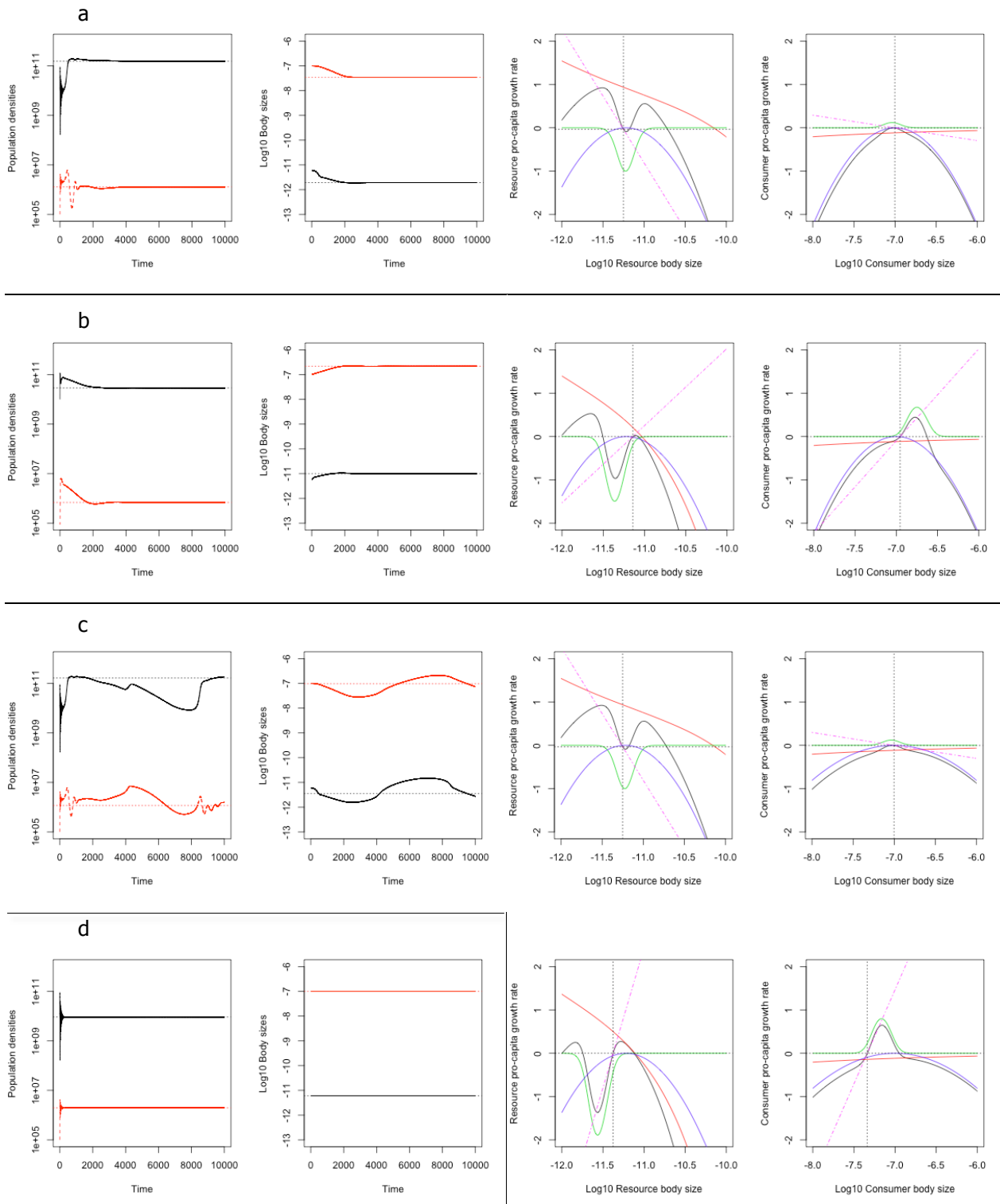
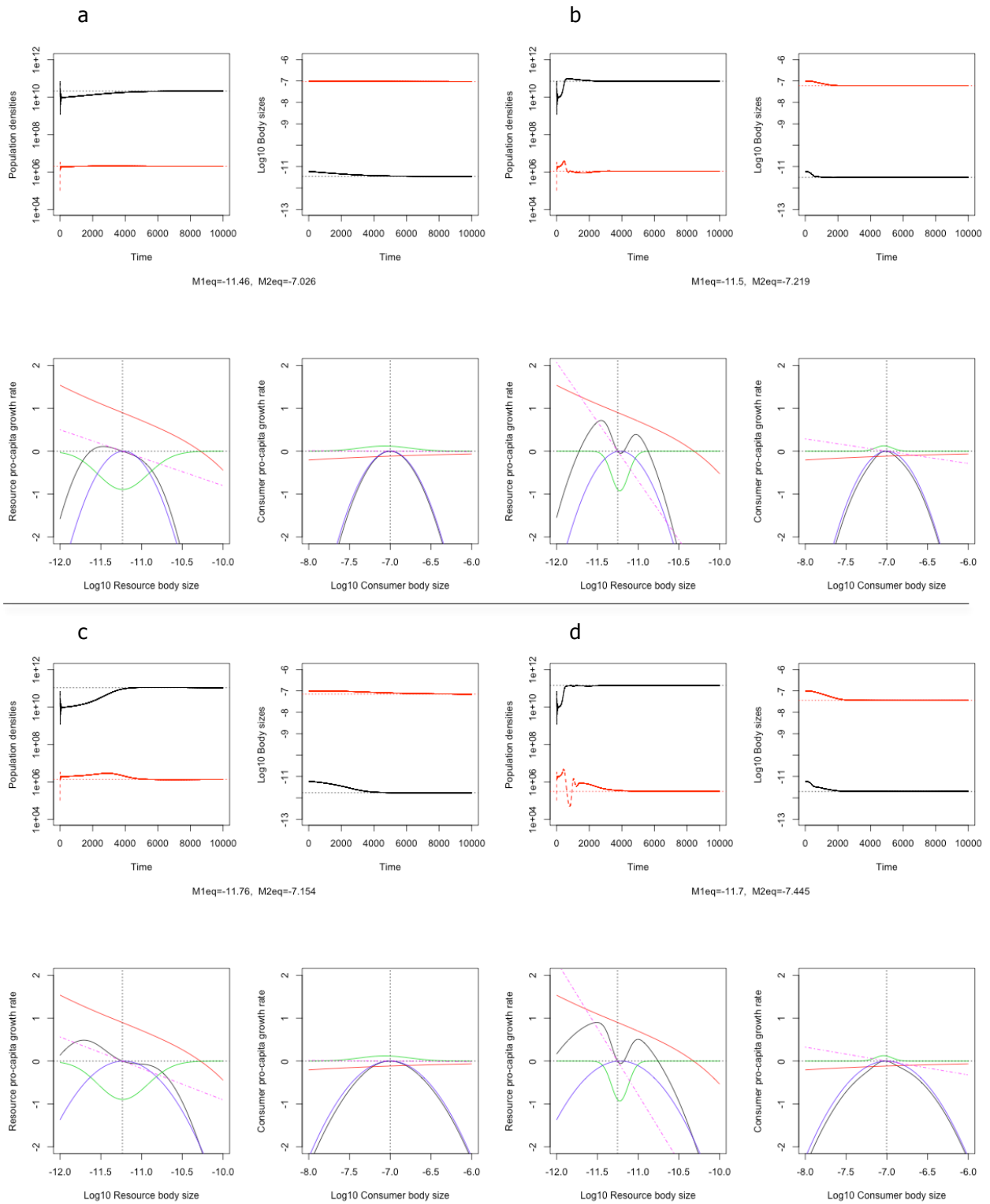


Figure 1



**Figure 2**

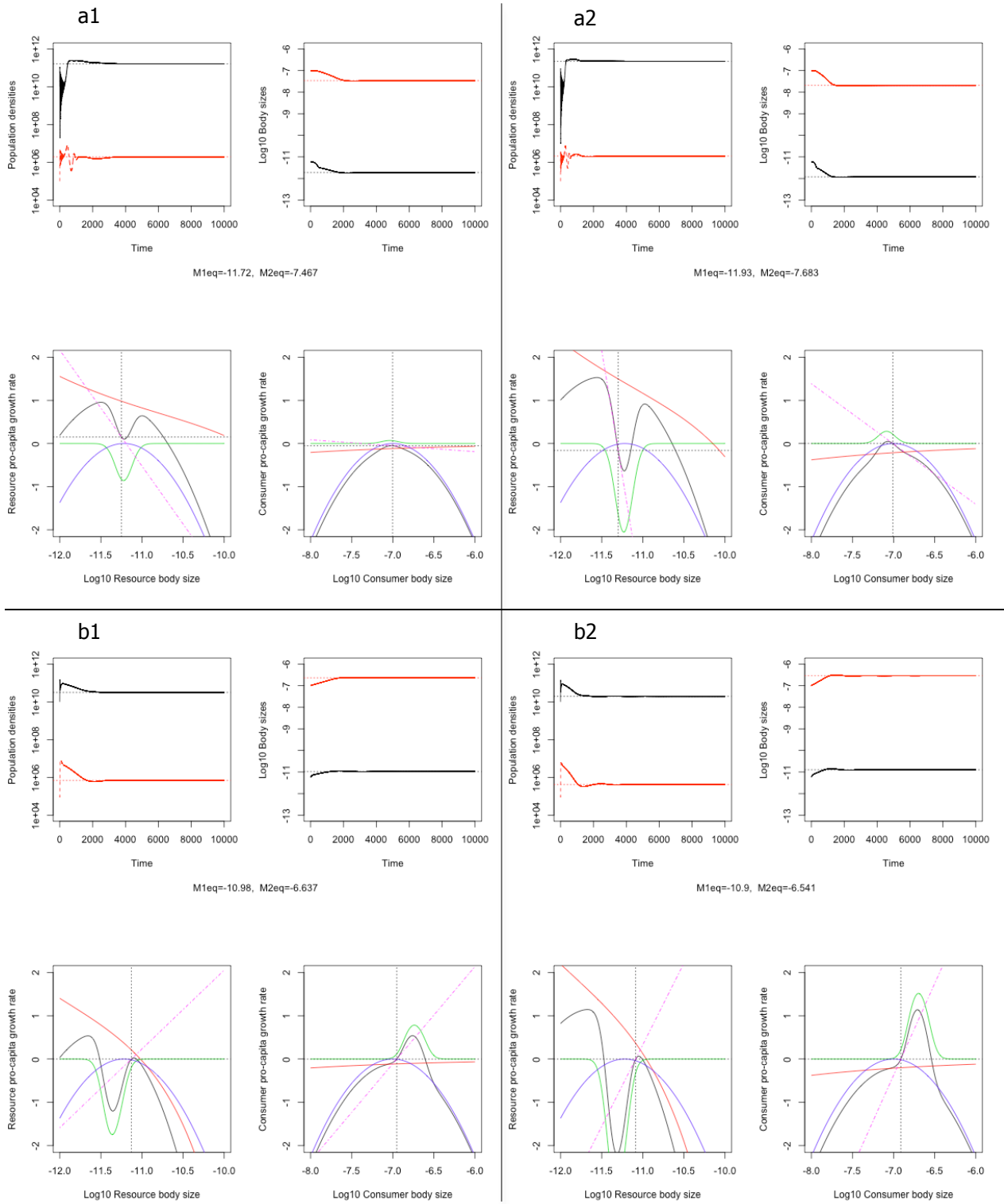


Figure 3 (part 1)

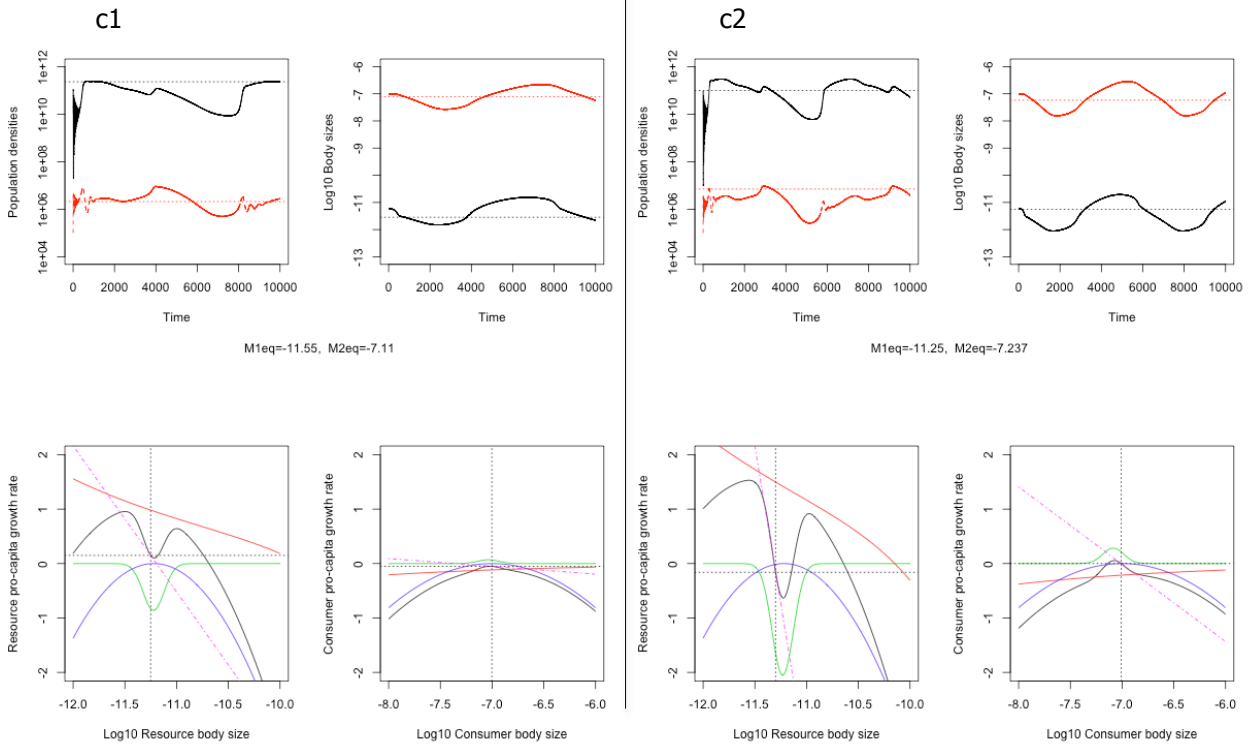


Figure 3 (part 2)

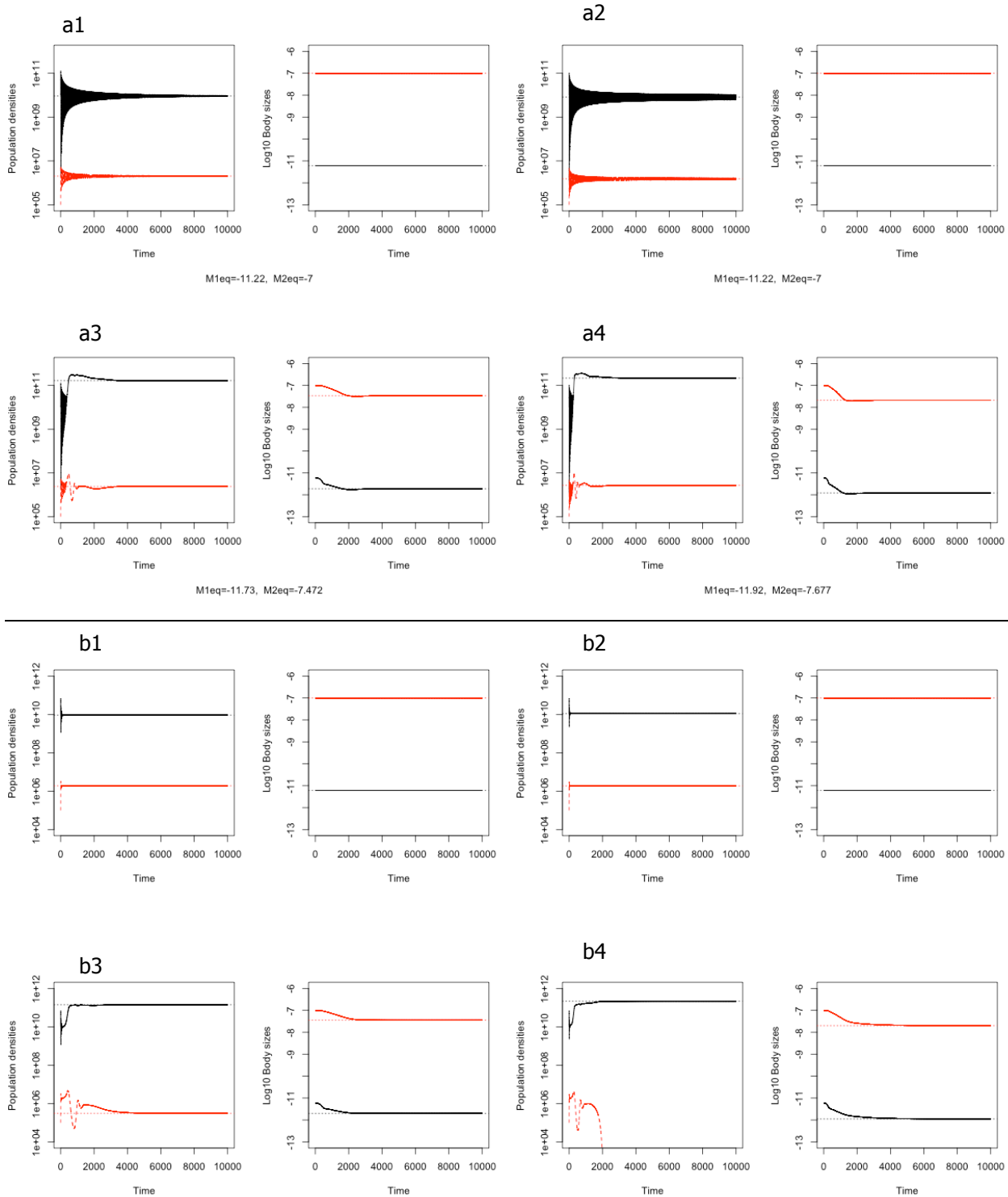


Figure 4

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## Appendix A: model derivation

### Basic ecological model in biomass density

The ecological model is based on a Lotka-Volterra model, improved with a logistic growth of the resource and a generalised type III functional response, and parameterized according to metabolic ecology relationships between physiological rates, body size (Yodzis & Innes, 1992) and temperature (Vasseur & McCann, 2005).

The basic equations, from Yodzis and Innes (1992), are the following:

$$\frac{dB_1}{dt} = (R_{\max} \hat{R} - J_{\max} \hat{J} B_2) B_1 \quad [1]$$

$$\frac{dB_2}{dt} = (-D + c J_{\max} \hat{J} B_1) B_2 \quad [2]$$

$B_1$  = biomass density of resource ( $\text{Kg m}^{-3}$ )

$B_2$  = biomass density of consumer ( $\text{Kg m}^{-3}$ )

The explanation of other terms is covered below.

#### Intrinsic growth of resource (R)

The growth function of resource is assumed to be a logistic curve. The biomass growth rate is maximal, equal to  $R_{\max}$ , when the resource biomass is 0, and approaches 0 when the resource biomass reaches its carrying capacity  $K$ . This is a simple and widely used way to take account of density-dependence in resource growth, and it is a key feature for the stability of the dynamic, as it produces stable equilibrium points instead of cycles.

$R_{\max}$  = maximum biomass intrinsic growth rate of resource, per unit biomass ( $\text{Kg Kg}^{-1} \text{year}^{-1}$ )

$\hat{R} = 1 - \frac{B_1}{K}$  = normalized biomass growth of resource, between 0 and 1 (non-dimensional) [3]

$K$  = carrying capacity of resource, in biomass density ( $\text{Kg m}^{-3}$ )

#### Consumption of resource by consumer (J)

The function for consumption is modelled by a generalised type III functional response, which takes account of resource density-dependence effects on consumption.



The resource ingestion rate, per unit biomass of consumer, is 0 when the resource biomass is 0, and increases according to a sigmoidal shape with the resource biomass, until a maximum value,  $J_{\max}$ . Type II functional response takes account of the saturation effect of the consumer when the resource is abundant, while type III allows also release from consumption pressure when the resource is rare. Interference competition of the consumer is not considered in the model, as competition for resource is assumed to be dominant.

Generalised III functional response has been demonstrated to be another important determinant of the stability of the system and has been included for this reason (Yodzis & Innes, 1992).

$J_{\max}$  = maximum biomass ingestion rate of consumer, per unit biomass (Kg Kg<sup>-1</sup> year<sup>-1</sup>)

$\hat{J} = \frac{B_1^q}{B_1^q + B_0^q} \frac{1}{B_1}$  = normalized generalised functional response type III (between 0 and 1), per unit biomass of resource (Kg<sup>-1</sup>) [4]

$B_0$  = half-saturation biomass density, or resource biomass needed to reach half-saturation of the consumer (Kg m<sup>-3</sup>)

$q$  = control parameter in functional response, if equal to 1 it gives a type II functional response, if equal to 2 it gives a type III functional response (non-dimensional)

$c$  = conversion efficiency of resource biomass to consumer biomass (non-dimensional)

The parameter  $f_e$  of Yodzis and Innes (1992) model, that represents the fraction of biomass removed from the resource population that is actually eaten, is neglected for model simplicity, by setting it equal to 1.

### Intrinsic loss of consumer (D)

The consumer biomass in absence of resource is assumed to decrease linearly over time, according to the rate  $D$ .

$D$  = intrinsic biomass loss rate of consumer, per unit biomass (Kg Kg<sup>-1</sup> year<sup>-1</sup>)

## Dependence of physiological rates on body size and temperature

The model is parameterized according to allometric relationships between physiological rates, body size (Yodzis & Innes, 1992) and temperature (Vasseur & McCann, 2005). This approach allows definition of a general model framework, valid for different species and extendible to multispecies systems by using relatively few parameters. At the same time, parameters values are constrained in a realistic way.

Biological rates scale according to a power law of body mass:  $y = \alpha m^\beta$ , where  $y$  is the rate,  $m$  is body size (Kg). The exponent  $\beta$  is around -1/4 for all organisms. The coefficient  $\alpha$ , instead, can be defined according to broad metabolic groups (Yodzis & Innes, 1992).

After body size, the variable that can explain the greatest part of the residual variation in metabolic rates is temperature (Gillooly et al. 2001). According to metabolic ecology recent advances, the relationship between physiological rates and temperature can be described by an exponential function:  $y = e^{-E/kT}$ , where  $E$  is the activation energy of the physiological process,  $k$  is the Boltzmann constant, and  $T$  is temperature in Kelvin.

$$R_{\max} = f_r a_r(T_0) m_1^{-\frac{1}{4}} e^{E_r(T-T_0)/kTT_0} = \text{maximum intrinsic biomass growth rate of resource, per unit biomass (Kg Kg}^{-1} \text{ year}^{-1}) \quad [5]$$

$$cJ_{\max} = f_j a_j(T_0) m_2^{-\frac{1}{4}} e^{E_j(T-T_0)/kTT_0} = \text{maximum biomass assimilation rate of consumer, per unit biomass (Kg Kg}^{-1} \text{ year}^{-1}) \quad [6]$$

$$D = a_d(T_0) m_2^{-\frac{1}{4}} e^{E_d(T-T_0)/kTT_0} = \text{intrinsic biomass loss rate of consumer, per unit biomass (Kg Kg}^{-1} \text{ year}^{-1}) \quad [7]$$

$a_r$  = maximum mass-specific intrinsic growth rate of resource (Kg Kg<sup>-1</sup> year<sup>-1</sup> Kg<sup>1/4</sup>)

$a_j$  = maximum mass-specific ingestion rate of consumer (Kg Kg<sup>-1</sup> year<sup>-1</sup> Kg<sup>1/4</sup>)

$a_d$  = mass-specific intrinsic loss rate of consumer (Kg Kg<sup>-1</sup> year<sup>-1</sup> Kg<sup>1/4</sup>)

$f_r$  = realized fraction (between 0 and 1) of maximum mass-specific intrinsic growth rate of resource (non-dimensional)

$f_j$  = realized fraction (between 0 and 1) of maximum mass-specific intrinsic growth rate of resource (non-dimensional)

$E_r$  = activation energy for intrinsic growth of resource (eV)

$E_j$  = activation energy for consumption (eV)

$E_d$  = activation energy for intrinsic loss of consumer (eV)

$T_o$  = standard temperature at which  $a_r$ ,  $a_j$  and  $a_d$  are measured (K)

$T$  = environmental temperature (K)

$k$  = Boltzmann constant (eV/K)

## Conversion of the model in individual densities

In order to incorporate evolution, it is sensible to track the dynamic of individual density instead of biomass density, because it is a variable independent on body size, thus the equations formulated for constant body size are still valid if evolution of body size is allowed. Moreover, in the evolutionary equation, it is needed to express fitness per individual.

Yodzis and Innes (1992) model is equivalent to conventional Lotka-Volterra models expressed in number of individuals, if populations are considered hypothetically made of fully grown individuals of the same size. According to this approximation, it is possible to assume:  $B_i = N_i m_i$ , where  $N_i$  is the individual density of species  $i$  ( $n\ m^{-3}$ ) and, under the condition of  $m_i$  constant, the following equations can be derived:

Resource:

$$\frac{dB_1}{dt} = \left( f_r a_r(T_o) e^{E_r(T-T_o)/kTT_o} m_1^{-\frac{1}{4}} \left(1 - \frac{B_1}{K}\right) - \frac{f_j a_j(T_o) e^{E_j(T-T_o)/kTT_o} m_2^{-\frac{1}{4}}}{c} \frac{B_1^q}{B_1^q + B_o^q} \frac{1}{B_1} B_2 \right) B_1$$

$$\frac{dN_1}{dt} m_1 = \left( f_r a_r(T_o) e^{E_r(T-T_o)/kTT_o} m_1^{-1/4} \left(1 - \frac{N_1 m_1}{K}\right) - \frac{f_j a_j(T_o) e^{E_j(T-T_o)/kTT_o} m_2^{-\frac{1}{4}}}{c} \frac{(N_1 m_1)^q}{(N_1 m_1)^q + B_o^q} \frac{1}{N_1 m_1} N_2 m_2 \right)$$

$$\frac{dN_1}{dt} = \left( f_r a_r(T_o) e^{E_r(T-T_o)/kTT_o} m_1^{-\frac{1}{4}} \left(1 - \frac{N_1}{\frac{K}{m_1}}\right) - \frac{f_j a_j(T_o) e^{E_j(T-T_o)/kTT_o} m_2^{-\frac{1}{4}}}{c \frac{m_1}{m_2}} \frac{(N_1)^q}{(N_1)^q + \left(\frac{B_o}{m_1}\right)^q} \frac{1}{N_1} N_2 \right) N_1$$

Consumer:

$$\frac{dB_2}{dt} = \left( -a_d(T_o) e^{E_d(T-T_o)/kTT_o} m_2^{-\frac{1}{4}} + c \frac{f_j a_j(T_o) e^{E_j(T-T_o)/kTT_o} m_2^{-\frac{1}{4}}}{c} \frac{B_1^q}{B_1^q + B_o^q} \frac{1}{B_1} B_1 \right) B_2$$

$$\frac{dN_2}{dt} m_2 = \left( -a_d(T_o) e^{E_d(T-T_o)/kTT_o} m_2^{-\frac{1}{4}} + c \frac{f_j a_j(T_o) e^{E_j(T-T_o)/kTT_o} m_2^{-\frac{1}{4}}}{c} \frac{(N_1 m_1)^q}{(N_1 m_1)^q + B_o^q} \frac{1}{N_1 m_1} N_1 m_1 \right) N_2 m_2$$

$$\frac{dN_2}{dt} = \left( -a_d(T_0)e^{E_d(T-T_0)/kTT_0}m_2^{-\frac{1}{4}} + c \frac{m_1}{m_2} \frac{f_j a_j(T_0)e^{E_j(T-T_0)/kTT_0}m_2^{-\frac{1}{4}}}{(N_1)^q + \left(\frac{Bo}{m_1}\right)^q} \frac{1}{N_1} N_1 \right) N_2$$

The new formulation of the model equations can be interpreted as follows:

$$\frac{dN_1}{dt} = (R_{n_{\max}} \widehat{R}_n - J_{n_{\max}} \widehat{J}_n N_2) N_1 \quad [8]$$

$$\frac{dN_2}{dt} = (-D_n + c_n J_{n_{\max}} \widehat{J}_n N_1) N_2 \quad [9]$$

$N_1$  = individual density of resource (n m<sup>-3</sup>)

$N_2$  = individual density of consumer (n m<sup>-3</sup>)

#### Intrinsic growth of resource:

$R_{n_{\max}}$  = maximum intrinsic individual growth rate of resource, per individual (n n<sup>-1</sup> year<sup>-1</sup>)

$$\widehat{R}_n = 1 - \frac{N_1}{K_n} = \text{normalized growth of resource (non-dimensional)} \quad [10]$$

$$K_n = \frac{K}{m_1} = \text{carrying capacity of resource, in individual density (n m}^{-3}\text{)} \quad [11]$$

#### Consumption of resource by consumer:

$J_{n_{\max}}$  = maximum ingestion rate of individuals per individual consumer (n n<sup>-1</sup> year<sup>-1</sup>)

$$\widehat{J}_n = \frac{N_1^q}{N_1^q + No^q} \frac{1}{N_1} = \text{normalized functional response generalised type III, per resource individual (n}^{-1}\text{)} \quad [12]$$

$No = \frac{Bo}{m_1}$  = half-saturation individual density, or resource individual density needed to reach half-saturation of consumer [13]

$q$  = control parameter in functional response

$$c_n = c \frac{m_1}{m_2} = \text{conversion efficiency of resource individuals in consumer individuals (non-dimensional)} \quad [14]$$

### Intrinsic loss of consumer:

$D_n$  = intrinsic loss rate of consumer per individual ( $n \text{ n}^{-1} \text{ year}^{-1}$ )

### Allometric relationships:

$R_{n \max} = f_r a_r (T_0) m_1^{-\frac{1}{4}} e^{E_r(T-T_0)/kTT_0}$  = maximum intrinsic individual growth rate of resource, per individual ( $n \text{ n}^{-1} \text{ year}^{-1}$ ) [15]

$c_n J_{n \max} = f_j a_j (T_0) m_2^{-\frac{1}{4}} e^{E_j(T-T_0)/kTT_0}$  = maximum individual assimilation rate of consumer, per individual ( $n \text{ n}^{-1} \text{ year}^{-1}$ ) [16]

$D_n = a_d (T_0) m_2^{-\frac{1}{4}} e^{E_d(T-T_0)/kTT_0}$  = intrinsic individual loss rate of consumer, per individual ( $n \text{ n}^{-1} \text{ year}^{-1}$ ) [17]

The parameters  $a_r$ ,  $a_j$ ,  $a_d$ ,  $f_r$  and  $f_j$  are defined as above, in the biomass model.

### Conversion to log of body sizes

In the ecological equations above, body size distribution is not necessary to describe the dynamic of the system. The only parameter needed is  $m$ , that can be considered as a representative value of the central tendency of body size in the populations. In order to include evolution of body size into the model, instead, the distribution of body size becomes relevant, as shown in the following paragraphs.

Body size distributions are typically skew to the right and the variance increases with the mean. A common way to deal with this issue is to model body size by using a log-normal distribution, in which the coefficient of variation is constant. Then, by transforming to the log scale, body size distribution becomes normal, and the variance is made independent on the mean. This has some important advantages. Firstly, it allows tracking the evolution of the arithmetic mean of the log-body size, that is a more correct measure of the central tendency for skew distributions than the arithmetic mean of body size. Secondly, it allows considering the variance parameters - that appear in consumer preference, stabilising selection and quantitative genetic equation - independent on the mean, so constant in time and, in the most simple hypothesis, equal for the two species.

The transformation is made by substituting  $m$  with  $10^M$ , where  $M$  is the log10 of body size.

Resource:

$$\frac{dN_1}{dt} = \left( f_r a_r(T_0) e^{E_r(T-T_0)/kTT_0} m_1^{-\frac{1}{4}} \left(1 - \frac{N_1}{K}\right) - \frac{f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} m_2^{-\frac{1}{4}}}{c \frac{m_1}{m_2}} \frac{(N_1)^q}{(N_1)^q + \left(\frac{Bo}{m_1}\right)^q} \frac{1}{N_1} N_2 \right) N_1$$

$$\frac{dN_1}{dt} = \left( f_r a_r(T_0) e^{E_r(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_1} \left(1 - \frac{N_1}{K}\right) - \frac{f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2}}{c \frac{10^{M_1}}{10^{M_2}}} \frac{(N_1)^q}{(N_1)^q + \left(\frac{Bo}{10^{M_1}}\right)^q} \frac{1}{N_1} N_2 \right) N_1$$

[18]

Consumer:

$$\frac{dN_2}{dt} = \left( -a_d(T_0) e^{E_d(T-T_0)/kTT_0} m_2^{-\frac{1}{4}} + c \frac{m_1}{m_2} \frac{f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} m_2^{-\frac{1}{4}}}{c \frac{m_1}{m_2}} \frac{(N_1)^q}{(N_1)^q + \left(\frac{Bo}{m_1}\right)^q} \frac{1}{N_1} N_1 \right) N_2$$

$$\frac{dN_2}{dt} = \left( -a_d(T_0) e^{E_d(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} + c \frac{10^{M_1}}{10^{M_2}} \frac{f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2}}{c \frac{10^{M_1}}{10^{M_2}}} \frac{(N_1)^q}{(N_1)^q + \left(\frac{Bo}{10^{M_1}}\right)^q} \frac{1}{N_1} N_1 \right) N_2$$

[19]

## Dependence of trophic link strength on relative body size

In the ecological framework of Yodzis and Innes (1992), the interaction strength between resource and consumer is fixed. According to many studies, body size seems to play a fundamental role in determining the interaction strength. A general finding is that the consumer tends to choose its resources according to a preferred consumer-resource body size ratio. The optimal ratio can be well described by broad habitat categories and consumer types (Brose et al. 2006).

In an evolutionary context, the dependence of trophic interactions on body size can produce a selective pressure and lead body size to evolve, and, vice versa, evolution of body size can change the interaction strength between species. For this reason, in order to study the eco-evolutionary dynamic of consumer-resource interaction, it is essential to explicit the dependence of interaction strength on body size.

The consumer preference can be modelled as a log-Gaussian function centred on an optimal consumer-resource body size ratio (Lewis et al. 2007), according to empirical evidence of consumer stomach content body size distribution.

$$z = e^{\left[ -\frac{(a - \log_{10}(\frac{m_2}{m_1}))^2}{2b^2} \right]} = e^{\left[ -\frac{(a - (M_2 - M_1))^2}{2b^2} \right]} \quad [20]$$

$a$  = log of the optimal consumer-resource body size ratio (non-dimensional)

$b$  = standard deviation of consumer preference, is a measure of diet breadth (non-dimensional)

Consumer preference can be considered as a measure of the effective proportion of resource population that a consumer can actually eat, because of a suitable body size:  $N_{1eff} = zN_1$ . Therefore, consumer preference can be easily incorporated into the model equations, by substituting  $N$  with  $N_{1eff}$  into the normalized functional response expression.

$$\hat{J} = \frac{N_{1eff}^q}{N_{1eff}^q + No^q} \frac{1}{N_1} = \frac{zN_1^q}{zN_1^q + No^q} \frac{1}{N_1} \quad [21]$$

This is also equivalent to assume that the attack rate (Williams et al. 2007) is proportional to consumer preference.

## Quantitative genetic equation

In the general energetic framework defined, body size is a critical trait that strongly affects consumer-resource interaction. Lots of studies have pointed out that body size can evolve over ecological time (Johnson & Stinchcombe 2007, Fussmann et al. 2007). Therefore, evolution of body size is included in the model in order to investigate the overall eco-evolutionary dynamic of the system.

Body size is a quantitative trait, determined by the additive effect of multiple loci.

A simplified quantitative trait equation is used, according to Iwasa (1991). The rate of change of mean trait in the population is proportional to the variation of the log of individual fitness in respect to the trait, calculated at the mean value of the trait. In a continuous time formulation, that considers overlapping generations, fitness is equal to the antilog of the instantaneous growth rate, leading to the equation:

$$\frac{d\bar{M}_i}{dt} = V_{ai} \frac{\partial \ln(W_i(M_i))}{\partial M_i} \Big|_{M_i=\bar{M}_i} = V_{ai} \frac{\partial \ln(e^{r_i(M_i)})}{\partial M_i} \Big|_{M_i=\bar{M}_i} = V_{ai} \frac{\partial r_i(M_i)}{\partial M_i} \Big|_{M_i=\bar{M}_i} \quad [22]$$

$\bar{M}_i$  = mean log-body size of species i

$W_i = e^{r_i}$  = individual fitness (of an individual of species i with body size  $M$ )

$r_i$  = individual per capita growth rate (of an individual of species i with body size  $M$ )

$M_i$  = individual body size (of an individual of species i)

$V_{ai}$  = genetic additive variance of species i ( $\log_{10}(K g^2)$ )

Quantitative trait equation is generally regarded as the most reliable model to study quantitative traits in a sexual population. In fact, it does not make any separation between ecological and evolutionary time, and it takes into account the intra-specific variation of the trait (Taper & Case, 1992). The simplified formulation used here is a limiting case of the general quantitative genetic recursion, when selection is assumed to be weak (the fitness of individuals has to be essentially constant over the bulk of the phenotypic distribution). This occurs when the variance of the trait is small compared to the variance of the fitness function (Iwasa et al. 1991). This approach has been used because it is computationally easier, as it does not require calculating integrals over the bulk of body size distribution, and also because it is not invalidated by fitness frequency-dependence (the fitness of a certain body size dependent on the body size distribution of the population).

In order to investigate how the energetic framework would affect the fitness and the evolution of body sizes, the formulation of the individual pro capita growth rate is directly derived from the ecological equations previously defined:

$$r_1(M_1) = a_r(T_0) e^{E_r(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_1} \left(1 - \frac{N_1}{K}\right) + \frac{1}{10^{M_1}} - \frac{f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2}}{c \frac{10^{M_1}}{10^{M_2}}} \frac{\left( e^{\left[ \frac{(a-(M_2-M_1))^2}{2b^2} \right]} N_1 \right)^q}{\left( e^{\left[ \frac{(a-(M_2-M_1))^2}{2b^2} \right]} N_1 \right)^q + \left( \frac{Bo}{10^{M_1}} \right)^q} \frac{1}{N_1} N_2 \quad [23]$$



$$\begin{aligned}
r_2(M_2) = & -a_d(T_0)e^{E_d(T-T_0)/kTT_0}10^{-\frac{1}{4}M_2} + \\
& + f_j a_j(T_0)e^{E_j(T-T_0)/kTT_0}10^{-\frac{1}{4}M_2} \frac{\left(e^{\left[-\frac{(a-(M_2-M_1))^2}{2b^2}\right]}\right) N_1^q}{\left(e^{\left[-\frac{(a-(M_2-M_1))^2}{2b^2}\right]}\right) N_1^q + \left(\frac{Bo}{10^{M_1}}\right)^q}
\end{aligned} \tag{24}$$

## Stabilising selection on body size

So far, only the metabolic selective pressure has been assumed to affect individual per capita growth rate, but in reality many others factors influence individual fitness. There is broad evidence that the multiplicative effect of various independent factors on fitness produce an overall stabilising selection on body size. Therefore, a background stabilising effect on fitness is considered to give a more realistic stability to the system. In particular, it is needed to prevent body size of resource to decrease to zero in absence of the consumer, because of the metabolic advantage of smaller sizes.

The stabilising selection effect can be simply added to the model by multiplying metabolic fitness function by a Gaussian function centred on an optimal body size,  $Mo$ :

$$W_{background} = e^{\left[-\frac{(Mo_i - \log_{10}(m_i))^2}{2v_i^2}\right]} = e^{\left[-\frac{(Mo_i - M_i)^2}{2v_i^2}\right]} \tag{25}$$

$$W_{itot} = W_i W_{ibackground} = e^{r_i} W_{ibackground} \tag{26}$$

$Mo_i = \log_{10}(mo_i) =$  optimal log-body size for species  $i$  ( $\log_{10}(\text{Kg})$ )

$v_i =$  standard deviation of stabilising selection on species  $i$  ( $\log_{10}(\text{Kg})$ )

This is equal to add a quadratic function to per capita growth rate:

$$r_{itot} = \ln(W_{itot}) = \ln(e^{r_i} e^{\left[-\frac{(Mo_i - M_i)^2}{2v_i^2}\right]}) = r_i - \frac{(Mo_i - M_i)^2}{2v_i^2} \tag{27}$$

## Normalisation of timescale

The complete model equations are the followings:

$$\frac{dN_i}{dt} = r_{itot}(\bar{M}_i)N_i \tag{28}$$

$$\frac{d\bar{M}_i}{dt} = V_{ai} \left. \frac{\partial r_{itot}(M_i)}{\partial M_i} \right|_{M_i = \bar{M}_i} \tag{29}$$

Resource per capita growth rate:

$$\begin{aligned}
r_{1tot}(M_1) = & f_r a_r(T_0) e^{E_r(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_1} \left(1 - \frac{N_1}{K}\right) + \\
& \frac{10^{M_1}}{10^{M_2}} \\
- & \frac{f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2}}{c \frac{10^{M_1}}{10^{M_2}}} \frac{\left(e^{\left[-\frac{(a-(M_2-M_1))^2}{2b^2}\right]}\right) N_1^q}{\left(e^{\left[-\frac{(a-(M_2-M_1))^2}{2b^2}\right]}\right) N_1^q + \left(\frac{Bo}{10^{M_1}}\right)^q} \frac{1}{N_1} N_2 + \\
& - \frac{(Mo_1 - M_1)^2}{2v_1^2}
\end{aligned} \tag{30}$$

Consumer pro capita growth rate:

$$\begin{aligned}
r_{2tot}(M_2) = & -a_d(T_0) e^{E_d(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} + \\
& + f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} \frac{\left(e^{\left[-\frac{(a-(M_2-M_1))^2}{2b^2}\right]}\right) N_1^q}{\left(e^{\left[-\frac{(a-(M_2-M_1))^2}{2b^2}\right]}\right) N_1^q + \left(\frac{Bo}{10^{M_1}}\right)^q} \\
& - \frac{(Mo_2 - M_2)^2}{2v_2^2}
\end{aligned} \tag{31}$$

A last refinement needed regards the model timescale. The speed of the dynamic varies greatly, depending on the speed of the physiological processes, ultimately depending on body sizes. In order to define a general timescale that is suitable for every system, all the rates in the model are normalized respect to the intrinsic growth rate of the resource (Yodzis & Innes, 1992; Vasseur & McCann, 2005). The transformation is made by dividing the equations by the intrinsic maximum growth rate of the resource at its optimal body size and temperature:

$$x = a_r(T_0) 10^{-\frac{1}{4}M_{o1}} \tag{32}$$

Then, the unit time is rescaled by defining a new time variable  $t'$  that is proportional to the intrinsic maximum growth rate of resource:

$$t' = xt = a_r(T_0) 10^{-\frac{1}{4}M_{o1}} \tag{33}$$

The timescale transformed equations are the following:

$$\frac{dN_i}{dt'} = r'_{i\text{tot}}(\bar{M}_i)N_i \quad [34]$$

$$\frac{d\bar{M}_i}{dt'} = V_{ai} \left. \frac{\partial r'_{i\text{tot}}(M_i)}{\partial M_i} \right|_{M_i = \bar{M}_i} \quad [35]$$

$$r'_{1\text{tot}}(M_1) = \left( \begin{array}{l} f_r a_r(T_0) e^{E_r(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_1} \left(1 - \frac{N_1}{K}\right) + \\ \frac{10^{M_1}}{10^{M_1}} \\ f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} \frac{(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1)^q}{(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1)^q + \left(\frac{Bo}{10^{M_1}}\right)^q} \frac{N_2}{N_1} + \frac{1}{a_r(T_0) 10^{-\frac{1}{4}M_{o1}}} \\ c \frac{10^{M_1}}{10^{M_2}} \\ -\frac{(M_{o1} - M_1)^2}{2v_1^2} \end{array} \right) \quad [36]$$

$$r'_{2\text{tot}}(M_2) = \left( \begin{array}{l} -a_d(T_0) e^{E_d(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} + \\ f_j a_j(T_0) e^{E_j(T-T_0)/kTT_0} 10^{-\frac{1}{4}M_2} \frac{(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1)^q}{(e^{\left[\frac{-(a-(M_2-M_1))^2}{2b^2}\right]} N_1)^q + \left(\frac{Bo}{10^{M_1}}\right)^q} + \frac{1}{a_r(T_0) 10^{-\frac{1}{4}M_{o1}}} \\ -\frac{(M_{o2} - M_2)^2}{2v_2^2} \end{array} \right) \quad [37]$$

The model can still be reduced to Vasseur and McCann's (2005) model if parameters are properly set in order to make not influent all the features progressively added to the model. To get this, consumer preference has to be equal to 1 ( $a = M_2 - M_1$ ), stabilising selection penalization has to be equal to 0 ( $M_i = M_{o_i}$ ), the functional response is made type II ( $q = 1$ ) and, most importantly, evolution of body size is forbidden ( $V_{ai} = 0$  or alternatively  $v_i = > 0$ ).

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## **PROJECT 2: FUNCTIONAL AND PHYLOGENETIC STRUCTURE OF SUBALPINE MEADOW PLANT COMMUNITIES**

### **Abstract**

Ecological similarity among species can shape the structure of biological communities, through habitat filtering and limiting similarity. The responses of species to these selective forces can be either ecological, i.e. habitat tracking and competitive exclusion, or evolutionary, i.e. adaptation to the environment and character displacement. In addition, different forces can shape community diversity along main environmental gradients.

The functional and phylogenetic structure of a pool of sub-alpine meadow plant communities, located in the South-west of Switzerland, has been studied in order to formulate some hypothesis on the processes involved.

The analysis combines the two main complementary methods currently used in literature: pairwise species correlations between functional, phylogenetic and niche distances and community metrics based on Rao index.

At global scale, functional clustering emerges, likely produced by habitat filtering. Otherwise, the traits responsible of the functional structure are moderately labile, and the phylogenetic structure is not different from random, suggesting a role of convergent evolution in shaping community structure.

Along the elevation gradient, clustered communities at low elevation suggest a possible role of land use in constraining community diversity.

The results could be taken into consideration in the development of niche models to predict community responses to global change.

## Introduction

Understanding how natural communities assemble and the forces that influence their dynamics, diversity and ecosystem function is an important objective to forecast and manage the ecosystem dynamics in face of the world-wide global change (Cavender-Bares *et al.*, 2009).

A high amount of studies in literature shows that the composition of communities is caused by a multitude of processes of different nature: niche, neutral and historical-biogeographical processes (Lortie *et al.*, 2004; Vamosi *et al.*, 2009). Niche theory, in particular, focuses on the importance of species ecological differences, represented by functional trait dissimilarity, in shaping the community structure. On the one hand, co-occurring species are expected to have similar traits, because selected in the same way by the environment. Filtering factors can be abiotic factors, like climate, but also biotic factors, like shared natural enemies or mutualists. On the other hand, the similarity of co-occurring species is expected to be limited because of the interactions among them. These include various negative interactions among similar species: direct and indirect competition, mediated by consumers, pathogens or mutualists, and positive interactions among different species as well (Cavender-Bares *et al.*, 2009).

The analysis of the functional structure of communities can give some indication on the niche processes involved in the shaping of community diversity: if the community structure is clustered (i.e. co-occurring species are more similar than expected by random processes) probably some kind of environmental filtering is constraining community diversity; otherwise, if it is overdispersed (i.e. co-occurring species are less similar than expected by random processes), limiting similarity is likely involved (Weiher & Keddy, 1995).

Another reason for the complexity of community assembly is that both ecological and evolutionary processes contribute to it (Parmesan, 2006; Berg *et al.*, 2009). Species responses to the selective forces produced by niche processes can be either ecological, i.e. habitat tracking and competitive exclusion, or evolutionary, i.e. adaptation to the environment and character displacement.

A qualitative indication of the relative importance of ecological vs. evolutionary processes can be inferred from the comparison between the functional and the phylogenetic structure of communities, and from the degree of conservatism of the traits that generate functional structure. In fact, if functional and phylogenetic structure

corresponds, and traits are conserved, species responses are more likely ecological. Otherwise, if the phylogenetic structure is weaker and traits are labile, evolutionary processes are probably involved (Silvertown *et al.*, 2006).

Understanding to which extent environmental filtering and species interactions influence the structure of natural communities, as well as the relative role of ecological and evolutionary processes, can be useful in developing theoretical frameworks for the prediction of community responses to environmental change. In particular, in the context of species distribution models (Guisan & Thuiller, 2005), it can help to establish whether it is possible to define "assembly rules" based on species similarity, in order to predict not only single species distribution, but also community composition. Functional or even phylogenetic similarity can in fact be related to the probability of co-occurrence of species. Moreover, species distribution models assume niche conservatism, i.e. the tendency of species niches to remain unchanged over time. The analysis of the phylogenetic structure of communities can help to understand the degree of reliability of this assumption (Pearman *et al.*, 2007).

Furthermore, the processes involved in community assembly are not expected to be uniform in the environment (Graham *et al.*, 2009). Understanding which forces shape functional and phylogenetic diversity along environmental gradients is important to predict future community assembly, especially if the environmental conditions are expected to shift along the gradient because of global change. In particular, it would be important to detect factors constraining community diversity, because it can be linked to various important ecosystem properties, i.e. productivity or ability to respond to environmental changes (Cavender-Bares *et al.*, 2009)

According to this framework, the functional and phylogenetic structure of a pool of sub-alpine meadow plant communities has been studied. The analysis combines the two main complementary methods currently used in literature: species correlations and community metrics (Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009). The work investigates the overall community structure of the study area, and the pattern of variation of community diversity along the main environmental gradient, represented by elevation. The main questions are: is there a significant signal in the community functional structure, which can suggest the importance of habitat filtering and limiting similarity? Is the phylogenetic structure similar to the functional structure, and are the functional traits conserved, or some degree of niche evolutionary lability can be detected? Is there a significant pattern of community diversity along the elevation gradient, able to suggest possible factors constraining community diversity?

## Materials and methods

A full description of the detailed materials and methods is in the Appendix A. Key features adopted are as follows.

### Community data

Diablerets study area (Fig. 1) is a 700 Km<sup>2</sup> area localised in the Swiss Prealps, and characterised by a strong elevation gradient (from 300 to 3000 m). Community data come from 868 plots of 2×2 m<sup>2</sup>, restricted to the open vegetation areas.

The analysis is based on three kinds of data: niche, functional trait and phylogenetic data. Niche data consist of measures of local abundance of species and environmental variables in each plot. Five topoclimatic variable are used: temperature degree days, moisture index, global solar radiation, slope, topographic position (Table 1(a)) (Randin *et al.*, 2010).

Functional trait data consist in mean species values of two traits: canopy height and leaf dry matter content (Table 1(b)), which are considered to be two of the most important axes of plant specialization (Evan *et al.*, 1999; Levorel *et al.*, 2007).

Phylogenetic data consist in *rbcl* nucleotide sequences.

The available species are 128 species, belonging to 114 genera and representing the 65% of the total vegetation cover of all the plots.

### Statistical analysis

Two complementary analyses, which represent the two main methods used in literature (Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009), are performed: species correlations and community metrics.

Both the analyses are based on measures of species dissimilarities.

Niche distances are calculated as 1- degree of overlap in the space of the topoclimatic variables, based on Schöner index (Broennimann *et al.*, in prep.).

Functional trait distances are calculated as Euclidean distances between mean species trait values.

Finally, phylogenetic distances are obtained from the Maximum Likelihood tree (Fig. 2), as sums of branch lengths.

Species correlations consist in the analysis of the concordance between functional, phylogenetic and niche distances among pairs of species (Vamosi *et al.*, 2009).

Pairwise distances are plotted against each other in all the tree possible combinations,

and the significance of the correlations is assessed by Mantel tests (Legendre & Fortin, 2010).

A positive correlation between functional (or phylogenetic) distances and niche distances indicates clustering in the functional (or phylogenetic) community structure. Otherwise, a negative correlation indicates overdispersion. Finally, a positive correlation between functional and phylogenetic distances identifies a phylogenetic signal.

Phylogenetic signal is also tested with variance of independent contrasts (Blomerg *et al.*, 2006), and its departure from Brownian motion expectation is assessed with K-statistic (Blomerg *et al.*, 2006).

Community metric analysis studies the indices of functional and phylogenetic diversity within single plots and along the elevation gradient.

The analysed plots are 320 plots, with 70% of the vegetation cover composed of species with available data.

The used index is Rao's quadratic entropy index, a measure of the expected functional (or phylogenetic) dissimilarity between two randomly chosen individuals in a plot (Bello *et al.*, 2010). The observed index is standardized respect to a random distribution of traits (or phylogeny) across all the plots (Kembel & Hubbel, 2006).

A negative functional (or phylogenetic) standardized Rao index indicates that the plot community is clustered respect to the pool of species of the study area. Likewise, a positive standardized Rao index indicates that the plot community is overdispersed respect to the pool of species of the study area.

The proportion of plots showing a structure significantly different from random is determined, and a Wilcoxon test is performed to assess if the mean diversity all over the plots is significantly different from random.

Functional and phylogenetic diversity are plotted against elevation and a linear model is used to assess if variation in plots diversity is significantly explained by elevation. Finally, functional and phylogenetic diversity are plotted against each other and the correlation is tested with Spearman's test.



## Results

### Species correlations

A significant positive correlation is found between topoclimatic niche distances and functional trait distances:  $r=0.22$  ( $p=0.002$ ), which indicates a clustered pattern in the functional structure of the study area community (Fig. 3(a)).

No significant relationship is instead found between topoclimatic niche distances and phylogenetic trait distances:  $r=-0.03$  ( $p=0.222$ ), which indicates that pattern in the phylogenetic structure is not different from random (Fig. 3(b)).

A significant positive relationship is also found between functional and phylogenetic distances:  $r=0.12$  ( $p=0.002$ ), which indicates phylogenetic signal of functional traits (Fig. 3(c)). The independent contrasts confirm that the phylogenetic signal found is significant: CH:  $p=0.02$ ; LDMC:  $p=0.001$ . The K statistic shows that the phylogenetic signal is anyway lower than expected from Brownian evolution of traits: CH:  $K=0.15$ ; LDMC:  $K=0.30$ .

Finally, the plot of phylogenetic distances against niche distances is coloured according to functional distances, in order to represent the (third) functional dimension and display qualitatively the tree relationships all together (green=lower than the 0.25 quantile of trait distance distribution, red=higher than the 0.75 quantile) (Fig. 3(d)). The plot shows that high trait distances (red) tend to be related both to high niche distances and high phylogenetic distances (concentrated on the right and the top of the plot). Nevertheless, the combination of these two weak correlations produces no direct correlation between niche and phylogenetic distances.

### Community metrics

The distribution of standardized Rao diversity indices, all over the 320 plots analysed, shows that functional diversity (Fig. 4(a)) is lower than the expected in more than 75% of the plots, while phylogenetic diversity distribution (Fig. 4(b)) is almost centred on the value expected from random distribution. The percentage of plots significantly different from random are: functional diversity: 16% clustered and 0% overdispersed; phylogenetic diversity: 12% clustered and 4% overdispersed.

The Wilcoxon test shows that the mean functional diversity is significantly lower than the expected from random distribution of traits in the plots:  $p= 2.2e-16$ , indicating clustering of plot communities respect to the whole study area. On the contrary, the mean phylogenetic diversity is not significantly different from the null expectation:  $p= 0.9665$ ,

indicating that, overall, the phylogenetic structure of the study area is not different from random. Both the results are consistent with the species correlation analysis.

Despite the different overall trends in functional and phylogenetic community structure, the correlation between functional and phylogenetic diversity, according to Spearman rank correlation, is significantly positive:  $r=0.2540302$  ( $p=4.505e-06$ ).

Both functional and phylogenetic diversity plotted against elevation (Fig. 5(a,b)) show a significantly positive trend: functional diversity: slope=0.00088, R-squared=0.18 ( $p=9.168e-16$ ); phylogenetic diversity: slope=0.00094, R-squared=0.07 ( $p=1.9e-06$ ). The significantly clustered plots (green) are more frequent at low elevation (below 1500 m).

Finally, functional and phylogenetic diversity are plotted against each other (Fig. 6), and plots are coloured according to elevation (green=lower than the 0.25 quantile of elevation distribution, red=higher than the 0.75 quantile). This plot shows only qualitatively the link between the tree variables: the plots at low elevation (green) tend to have lower functional and phylogenetic diversity than the plots at high elevation (red).

## Discussion

### Community patterns at large scale

The patterns emerging at the study area scale are weak but consistent according to the species correlation and community metric analysis. This makes possible to formulate some hypothesis regarding the main processes acting at large scale.

The functional structure of the community is significantly clustered. Otherwise, the phylogenetic structure is overall not significantly different from random.

This pattern suggests that the process of habitat filtering is relatively more important than other processes in determining the community structure at the study area scale. Considering that the spatial scale is small compared to biogeographical processes, it is reasonable that species distributions reflect the environmental conditions, mediated by functional traits, more than biogeographical processes of speciation and dispersal limitation. Moreover, as the habitat variation in the study area is strong along the elevation gradient, habitat filtering is likely more relevant than limiting similarity or random demographic processes in shaping community composition.

As species interact with the environment via their phenotype, the association between phylogeny and habitat should be mediated by functional traits. The fact that the phylogenetic structure is overall much weaker than the functional structure suggests that the response of the species to habitat filtering is at least partially evolutionary. In particular, considering that the phylogenetic scale is big, it is likely to have some degree of convergent evolution, which would confuse the phylogenetic pattern respect to the functional one. The degree of phylogenetic signal, significant but lower than expected by Brownian evolution of traits, confirms the hypothesis of partial lability of traits along the phylogeny.

The fact that phylogenetic structure is overall much weaker than the functional structure does not prevent to have a weak but significant positive correlation between functional and phylogenetic diversity, consistent with the presence of a moderate phylogenetic signal, and detectable if community structure is analysed in single plots.

In order to better understand the relationship between phylogeny and habitat, it would be interesting to investigate whether traits are more conserved if smaller clades are considered, and to fit different models of character evolution, i.e. Brownian and Ornstein-Uhlenbeck (OU), in order to test for adaptive evolution of different lineages on

the same selective optima (Butler & King, 2004).

For a more exhaustive analysis, the improvement of the functional and the phylogenetic databases is crucial. Considering other functional traits would be important to better represent the multidimensional space of plant specialization, and eventually test if different traits are preferentially associated to different processes. It would be particularly important to increase the phylogenetic database, especially by sequencing some important alpine species that are lacking in GenBank.

## Community patterns along the elevation gradient

The study of the diversity pattern along the main environmental gradient of the study area shows that both functional and phylogenetic diversity are significantly positively correlated to elevation, with many significantly clustered plots concentrated at low elevation. This suggests that there is some factor constraining functional and phylogenetic diversity at low elevation more than at high elevation.

This result is at first sight quite surprising, considered similar studies on community structure along elevation gradients, which found clustering at high elevation, associated to extreme climatic conditions (Graham *et al.*, 2009). Nevertheless, a possible explanation can be formulated if one considers not only how climate changes along the elevation gradient, but also land use.

Low-elevation clustering could indicate that various filtering factors related to land use (i.e. herbivores, fertilization and grass-cut), as well as higher disturbance regimes associated with limited dispersal, could reduce functional (and consequently phylogenetic) diversity within these communities. High elevation plots, instead, could show higher within-community diversity because they are generally less affected by human land use. In addition, very few plots are above the 2000 m altitude, where the climatic conditions start to be harsh and limiting for plants and are expected to produce habitat filtering.

To test this hypothesis, high-resolution data on land cover, or better, direct estimation of the land use of the plots is needed.

To be noticed, the within-plot diversity ( $\alpha$ -diversity) is found to increase with the elevation, but the between-plot diversity ( $\beta$ -diversity) would not necessarily follow the same pattern. This could be tested by partitioning Rao's index in  $\alpha$ ,  $\beta$ , and  $\gamma$  components (De Bello *et al.*, 2009).

## Detecting limiting similarity

A small-scale analysis could be also important, in order to investigate the role of species

interactions and limiting similarity processes in the structuring of the study area communities. Limiting similarity did not emerge at large scale; otherwise it is suggested to be quite important in sub-alpine communities (Lortie et al., 2004).

Different kinds of analysis could be done to study the within-habitat community pattern. It is possible to reduce the regional pool, by considering only species that live in similar habitats, or it is possible to constrain the randomization, by permutation only between species that share similar habitats (environmental-constrained randomization, Peres-Neto et al., 2000). In both the cases, the basic idea is to define, as null hypothesis, a random distribution of traits (or phylogeny) within habitats, and not within the whole study area. Preliminary analyses did not show significant results, however the topic requires further investigation.

Other two simple improvements to test limiting similarity could be: consider more traits, as species could be specialized along different axes, and take into account local abundance of species in the measure of niche dissimilarity, as presence-absence is less informative regarding species interactions. It might be also necessary a more dense sampling in the environmental space, i.e. more plots located in similar habitats, or a more dense sampling in the phylogenetic tree, i.e. more closely-related species.

## Conclusions

The work represents a preliminary analysis on the main patterns and processes that drive the community structure of sub-alpine plants communities. Anyway, some general hypothesis can be drawn.

At global scale, the importance of functional clustering emerges, probably produced by habitat filtering. In addition, there is a moderate degree of evolutionary lability of the functional traits responsible of the functional structure, and a confused phylogenetic structure. This suggests that convergent evolution could play a role in shaping the community structure.

Along the elevation gradient, there is a possible role of land use in constraining within-communities diversity at low elevation.

Integrated with further analysis, the present results could be helpful in the definition of the important factors to be considered in the prediction of the responses of sub-alpine plant communities to global change.

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## Figures and tables

**Table 1.** a, b) Environmental variables and c) functional traits used in the analysis.

**Fig. 1.** Diablerets study area, with indication of sampling points, and its location in Europe.

Table 1. Environmental variables used a) in the species correlation analysis and b) in the community metric analysis; c) functional traits used in both the analysis.

**Fig. 2.** Maximum likelihood phylogenetic tree based on rbcL, with node supports.

**Fig. 3.** Species correlation analysis. Standardized pairwise species distances between 128 species plotted against each other (the slope of the red lines is equal to the correlation coefficient):

- a) functional trait distances plotted against topoclimatic niche distances;
- b) phylogenetic distances plotted against topoclimatic niche distances;
- c) functional trait distances plotted against phylogenetic distances;
- d) phylogenetic distances plotted against topoclimatic niche distances, and coloured according to functional traits distance values (green=lower than the 0.25 quantile of trait distance distribution, red=higher than the 0.75 quantile).

**Fig. 4.** Community metric analysis. Boxplot of the standardized Rao indices of a) functional and b) phylogenetic diversity, calculated for 230 plots. The red line is the expected functional diversity under the null hypothesis of random distribution of traits/phylogeny in the plots.

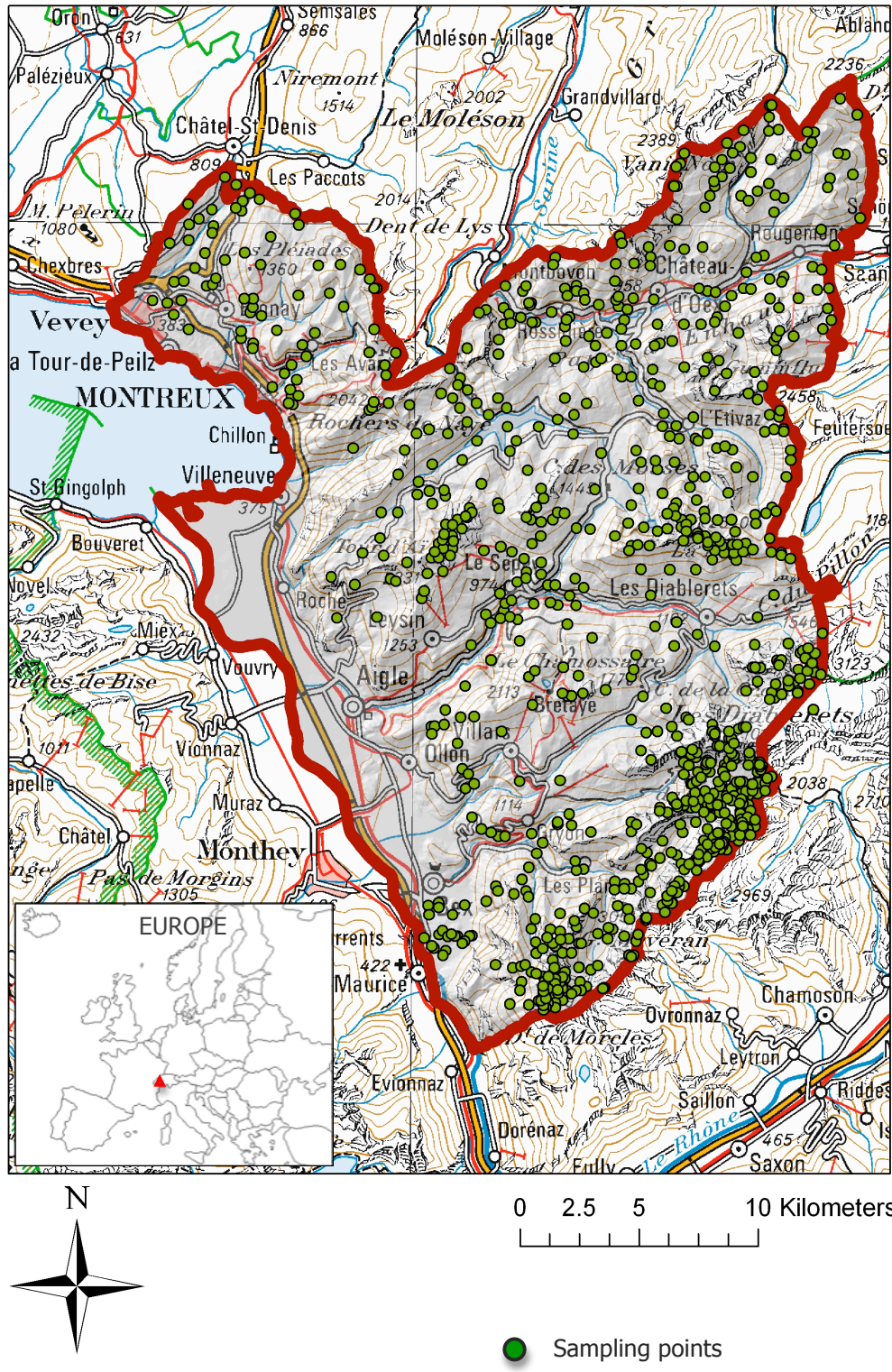
**Fig. 5.** Community metric analysis. Standardized Rao indices of a) functional and b) phylogenetic diversity are plotted against elevation. The black lines represent the linear models. The green points represent the significantly clustered plots (Rao index lower than the 0.025 quantile of the null distribution); the red points represent the significantly overdispersed plots (Rao index higher than the 0.975 quantile of the null distribution).

**Fig. 6.** Community metric analysis. Standardized Rao index of functional diversity plotted against standardized Rao index of phylogenetic diversity. The black line is proportional to the correlation coefficient. The colour represents plot elevation (green=lower than the 0.25 quantile of elevation distribution, red=higher than the 0.75 quantile).

| Variables                                    | Units                                 | Details  |
|--|---------------------------------------|--|
| <b>a) Topographic and climatic variables</b> |                                       |  |
| Temperature degree days                      | °C day year <sup>-1</sup>             | Sum of days with temperature >0, multiplied by daily mean temperature  |
| Moisture index                               | mm day                                | Monthly average of daily water balance (precipitation-potential evapotranspiration), in the growing season (June-August) |
| Global solar radiation                       | kJ m <sup>-2</sup> year <sup>-1</sup> | Daily global solar radiation   |
| Slope  | degrees                               | Slope inclination  |
| Topographic position                         | -                                     | Concave (-) vs. convex (+) land surface  |
| <b>b) Indirect environmental variables</b>   |                                       |  |
| Elevation                                    | m                                     | Altitude   |
| <b>c) Functional traits</b>                  |                                       |  |
| Canopy height (CH)                           | mm                                    | Distance between the highest photosynthetic tissue and the base of the plant   |
| Leaf dry matter content (LDMC)               | -                                     | Measure of tissue density, 1000 times the ratio between dry leaf mass and fresh leaf mass                                |

**Table 1**

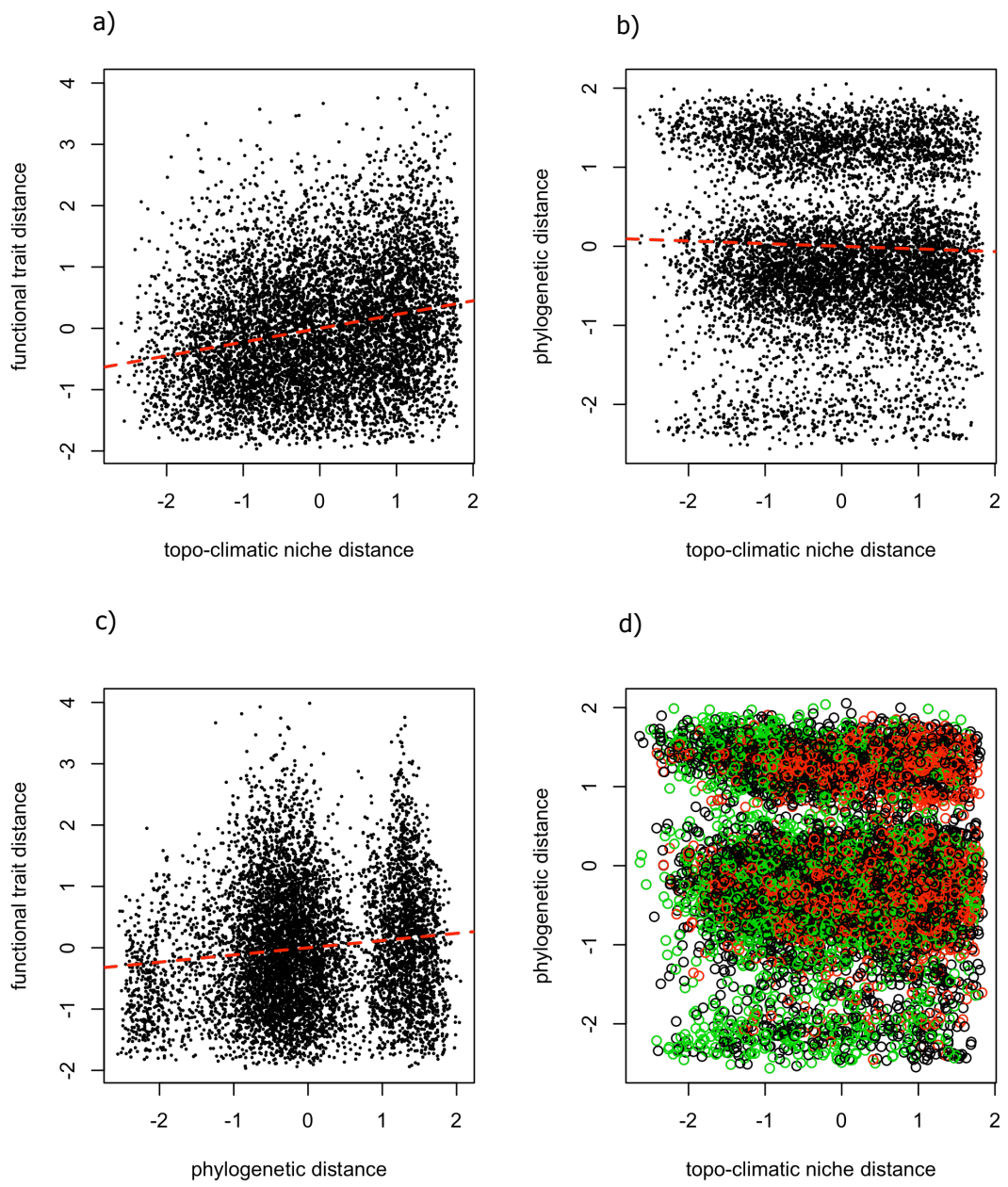




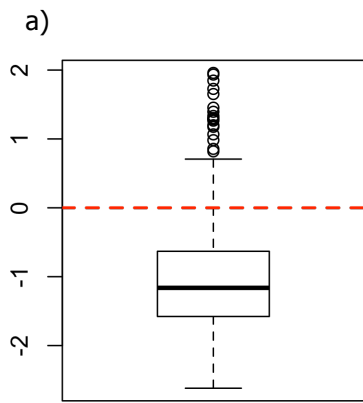
**Fig. 1**



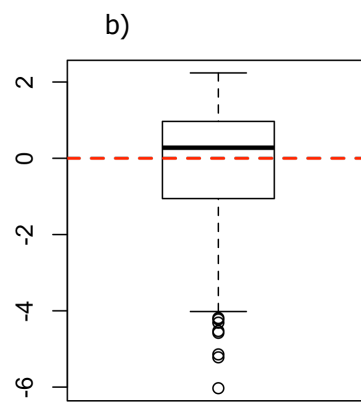
Fig. 2



**Fig. 3**

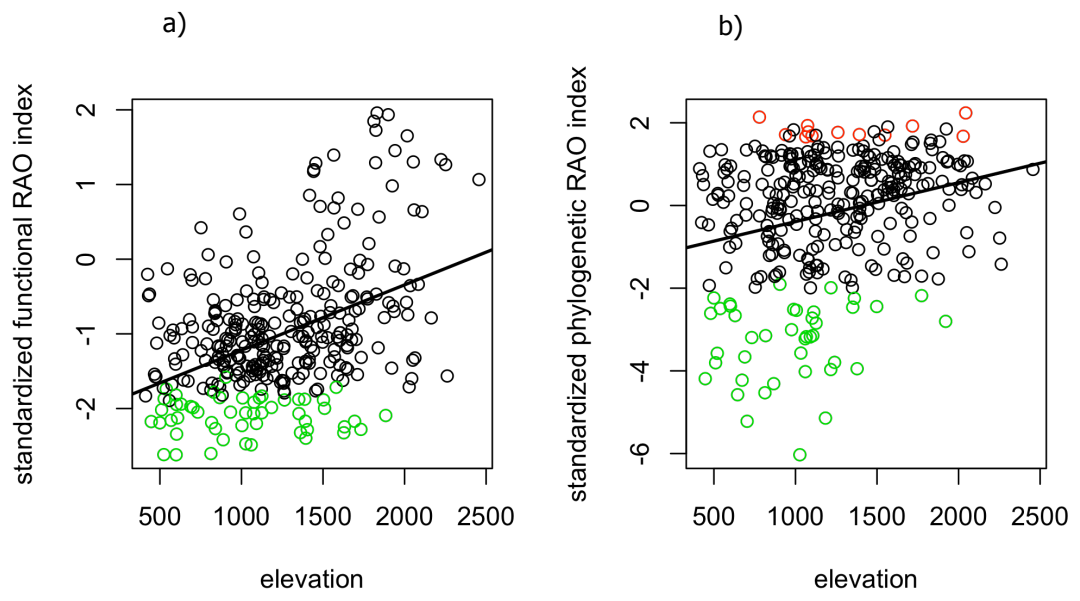


standardized functional RAO index

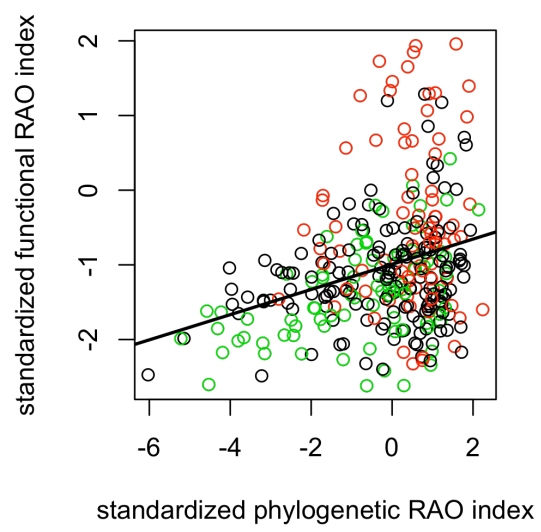


standardized phylogenetic RAO index

**Fig. 4**



**Fig. 5**



**Fig. 6**

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## Appendix A: full materials and methods

### Community data

#### *Study area*

The Diablerets study area (Figure 1) is localized within the north-western Prealps, in the Canton of Vaud, Switzerland (EU) and covers more than 700 Km<sup>2</sup> (46°10' to 46°30' N, 6°60' to 7°10' E). The elevation ranges from 375 m to 3,210 m, the annual mean temperature and the total precipitation vary respectively from 8°C and 1,200 mm at 600 m elevation to -5°C and 2,600 mm at 3,000 m elevation.

#### *Niche data*

Species abundances and environmental variables data are extracted from the Ecospat dataset of the University of Lausanne (Randin et al., 2010). The sampling points are 868 plots of 2x2 m<sup>2</sup>, restricted to the open vegetation areas and distributed according to a stratified sampling design respect to elevation, slope and topographic position. The minimum distance between plots is high enough to avoid spatial autocorrelation.

The abundance data are available for all the species occurring in each plot, for a total of 864 species. The abundances values are the medians of the Braun-Blanquet classes, i.e. they are a semi-quantitative measure of the percentage of area covered by the species in exam (levels: 0.01, 0.2, 3.15, 35.5, 62.5 and 87.5%). Subspecies data have been merged.

The environmental variables (Table 1.a) are five topographic and climatic variables considered to have a high eco-physiological significance: temperature degree days, moisture index, global solar radiation, slope and topographic position. The climatic variables derive from the Swiss national meteorological station network by spatial interpolation on a 25 m digital elevation model, while the topographic variables are directly derived from the DEM (Randin et al., 2010).

In addition, plot elevation (Table 1.b) is extracted to have a measure of the main indirect gradient of the study area. In fact, it explains most of the environmental variability of the area, as shown by the strong correlation between elevation and the first axis of the principal component analysis of the topoclimatic variables:  $r=-0.86$  ( $p=2.2e-16$ ).

### *Functional traits data*

Functional traits data (Table 1.c) are a preliminary subset of a wider ongoing field survey on several traits.

The sample traits are canopy height (CH) and leaf dry matter content (LDMC). They are chosen as they are quick-to-measure key traits often used to represent two of the main axes of plants specialization (Evan *et al.*, 1999; Levorel *et al.*, 2007). In particular, both of the traits are involved in stress tolerance to abiotic (i.e. temperature and water balance) and biotic factors (i.e. herbivores), and in plant competition (different strategies of light uptake and exploitation of resources).

The species data are obtained by averaging 10 measurements of single individuals sampled from different locations. The locations are previously chosen in order to represent most of the variation of the environmental conditions experienced by the species in their geographical ranges. The measurements are performed according to the standardized procedure of the LEDA traitbase (Kleyer *et al.*, 2008), the free-access database of life history traits of Northwest European flora.

As the number of flowering plant species of the area is very high, and many of them are very difficult to find (the abundance distribution follows a negative power law), only the species that are the most important in determining the actual community composition have been sampled. The species are chosen according to a local abundance criterion: a species has to be part of the main species that compose the 80% of the vegetation cover, in at least one plot. The list of species obtained (around 250 species) is then evaluated against global abundance and occurrence ranks all over the area. The concordance with these criteria is qualitatively confirmed.

All the used species have a number of occurrences higher than the locally defined standard threshold of 20 occurrences, except 10 species with a number of occurrences between 10 and 20, which were kept because of high local abundance. The selected species represent the 90% of the total vegetation cover of the area.

A preliminary analysis has also been done to evaluate whether to merge the field measurements with the data available in the LEDA database, in order to increase the number of species and/or the number of traits available for the analysis. The correlation between field measurements and LEDA data was acceptable (CH:  $r=0.62$ ,  $p= 2.896e-05$ ,  $n=38$ ; LDMC:  $r=0.84$ ,  $p= 4.776e-11$ ,  $n=37$ ). In addition, the correlation analysis on 50 species sourced from LEDA and several traits (Canopy height, Leaf dry matter content, Specific leaf area and Seed mass) gave results similar of those shown here. Anyway, the number of species available in LEDA would be limited and biased by elevation (high elevation plants under-represented). Consequently, the analysis shown here is based only on field measurements for the sake of consistency.

### *Phylogenetic data*

Phylogenetic reconstruction is based on the Ribulose-1,5-bisphosphate carboxylase/oxygenase plastid gene, large subunit (*rbcl*), as it is a slowly-evolving gene, widely used for the estimation of large plants phylogenies.

The phylogenetic data represent a preliminary subset obtained from GenBank database, which will be expanded by the sequencing of the lacking species.

Only 81 species, of the 250 with available traits, have been found in GenBank (for a total of 67 genera and a total abundance of 54% of the total cover of the area).

In order to increase the number of species available for the analysis, a substitute sequence has been assigned to the most abundant species of each genera not represented, by choosing an available sequence of another species belonging to the same genus. This procedure has been adopted because it should not affect significantly the calculation of inter-genera species distances. Therefore, 47 species, belonging to as many genera, were added. The final list of species is composed by 128 species, 114 genera and covers the 65% of the total vegetation of the area. Nevertheless, species correlation and community metrics analysis, performed on the 81 original species, resulted to be overall qualitatively similar to the analysis on the bigger pool of species.

### Statistical analysis

In order to study the functional and phylogenetic structure of the grassland communities in the study area, the two main methods used in literature are adopted: species correlations and community metrics (Cavender-Bares *et al.*, 2009).

Both of them are based on measures of pair-wise measures of species dissimilarities, calculated as described in the next paragraph.

#### Calculation of species distances

##### *Niche distances*

Niche distances are obtained by measuring the degree of overlap of species ranges projected in the space of the topo-climatic variables (Broennimann *et al.* in prep.). A principal component analysis, with standardization of the variables, is firstly performed to define which are the main axes that describe the most part of the topo-climatic variation among the plots. The occurrences of each pair of species are then projected into the environmental space described by the relevant PCA axes. By gridding this environmental space and using kernel density estimation, the density of occurrence of each species is obtained for each environmental condition (grid cell). The degree of overlap is measured by applying the Schöner's index (Schöner, 1970):

$$overlap = 1 - \left( \frac{1}{2} \sum_{x=1}^n |p_{xi} - p_{xj}| \right),$$

where  $n$  is the number of grid cells and  $p_{xi}$  and  $p_{xj}$  are the opportunely rescaled occurrence density of the two species in each grid cell.

Niche distances are measured as 1-overlap (0: complete overlap, 1: no overlap).

The analysis, performed with Schönner's measure of niche overlap directly applied on species occurrences, gave consistent results. Topo-climatic niche overlap was used because more informative, as it makes possible to link species distribution to specific environmental variables.

### *Functional distances*

Functional trait distances are calculated as Euclidean distances between the mean

species traits:  $d_{i,j} = \sqrt{\sum_{x=1}^n (t_{xi} - t_{xj})^2}$ , where  $n$  is the number of traits and  $t_{xi}$ ,  $t_{xj}$  is the

mean value of the trait for the species  $i$  and  $j$ , opportunely calculated as follows.

Firstly, traits are log-transformed, in order to make species dissimilarity based on the ratio between species traits. This is a simple solution for skewed trait distributions and is often considered more ecologically meaningful than using the traits difference in functional diversity studies (Leps *et al.*, 2006).

Then, a principal component analysis, with standardization of the traits is performed in order to keep the independent trait axes that explain the most of the variation in the functional multidimensional space. Euclidean distance is calculated on these axes. To be noticed, CH and LDMC already represents orthogonal (independent) axes, anyway the general procedure described above has been preferred because easily extendible to different traits.

As distances derived from single traits gave overall qualitatively similar results, distances based on a combination of traits have been preferred, in order to highlight the general trend that emerges in species functional dissimilarity.

### *Phylogenetic distances*

Phylogenetic distances are calculated as the sum of branch lengths (i.e. mean amount of molecular change per site) of the phylogenetic tree obtained by maximum likelihood (Figure 3), with *Picea abies* specified as the outgroup. The alignment and the maximum likelihood reconstruction are made with Sea View (Gouli *et al.*, 2010).

The evolutionary model used is the generalized time reversible (GTR) substitution model. The rate of change by site is modelled with a gamma distribution, with 4 categories and the parameter  $\alpha$  estimated from the data, in order to deal with the heterogeneous rates

of *rbcL* evolution. The heuristic search method is set as the best between Nearest Neighbour Interchange (NNI) and Sub-tree Pruning Regrafting (SPR) and the starting tree is the Neighbour Joining tree. The branch support is calculated by bootstrap with 100 replicates.

Few nodes have a low support, but the structure of the tree is overall qualitatively consistent with the accepted relationships among families (APG III) (Bremer *et al.*, 2009).

### Species correlations: analysis of concordance between functional, phylogenetic and niche distances between species

This method focuses on species as study objects. It makes possible to investigate how species are distributed into the environment respect to each other, and therefore to assess if their distribution follows to some functional and/or phylogenetic criteria based on species similarity.

The method is based on plotting pair-wise species distances (functional or phylogenetic) against niche distances. The correlation coefficient provides information on the overall pattern of community structure observed within the study area: if species distances are significantly positively correlated with niche distances, the species are clustered into the environment; otherwise, if the correlation is significantly negative, the species are overdispersed.

In addition, the relationship of pair-wise functional distances and phylogenetic distances is tested to assess if traits display a phylogenetic signal (significant positive correlation) or are labile (no correlation or negative correlation). A K statistic (Blomerg *et al.*, 2006) is also performed to assess if the phylogenetic signal is significantly higher ( $K > 1$ ) or lower ( $K < 1$ ) than expected from Brownian evolution of traits (function multiPhylosignal in Picante R package).

### *Null models*

Standard methods to assess the significance of the correlations would be inappropriate because the pair-wise distances are not mutually independent. Therefore, a permutational regression approach, based on Mantel test algorithm (Legendre & Fortin, 2010), is used.

The null model distribution is obtained by randomizing the community data in order to remove all (but only) the effect of the mechanism under study, i.e. the effect of species functional or phylogenetic identity on community composition (Vamosi *et al.*, 2009). The randomization consists in the permutation of rows and columns of one of the distance matrices, while the other distance matrix is kept unchanged. This is equivalent to randomize species identities (functional or phylogenetic) and keep unchanged their distribution in the environment. In the same way, for the traits distances vs. phylogenetic distances correlation, one of the two matrices is randomized respect to the other. This can be interpreted as permuting species traits over the tips of the phylogeny. The randomization is repeated 1000 times.

The null hypothesis is rejected if the observed correlation coefficient falls into the critical region of 5%. Regarding the correlations between functional or phylogenetic distances and niche distances, as aim is to detect either a positive or negative correlation, two-tails tests are performed. The correlation is considered significantly positive (negative) if the observed value is higher than the 0.975 quantile (lower than the 0.025 quantile) of the null distribution. For the traits distances vs. phylogenetic distances correlation, a one-tail test is used, as the goal is to detect a positive correlation. It is considered significant if the observed value is higher than the 0.95 quantile of the null distribution.

The relationship between traits and phylogeny has been assessed also by variance of independent contrasts (Blomerg *et al.*, 2006). If the  $p$  value is lower that 0.05, there is a significant phylogenetic signal (function multiPhylosignal in Picante R package).

### Community metric: analysis of functional and phylogenetic diversity within communities along environmental gradients

This method focuses directly on communities. It is aimed at assessing whether functional and/or phylogenetic diversity within communities is higher or lower than expected by random processes, and to test if this follows a pattern along some environmental gradients.

Many metrics are available for the quantification either of functional or phylogenetic diversity. The Rao's quadratic entropy index, is chosen as it is the only existing estimator of diversity that can be used with different measures of species dissimilarity (functional

or phylogenetic) and take into accounts relative species abundances (de Bello *et al.*, 2010). The Rao index is the sum of dissimilarities between all possible pairs of species in a community, weighted by the product of relative species abundances:

$$Rao = \sum_{i=1}^s \sum_{j=1}^s d_{ij} p_i p_j$$

, where  $s$  is the number of species in the community,  $d_{ij}$  is a measure of dissimilarity between to species  $i$  and  $j$  and  $p_i$   $p_j$  are the relative frequencies of the two species within the community.

Rao index represents the expectation of dissimilarity between two randomly chosen individuals in the community and it is a generalization of Simpson species diversity index (Rao index reduces to Simpson index when species distances are equal to 1).

If Rao index is significantly lower than expected by random processes, the community structure is clustered, while if it is higher, the community structure is overdispersed.

The analysis is performed on all the plots in which at least the 70% of the vegetation cover is composed of species with available data (320 plots). This threshold is chosen because it is not much lower than the 80% threshold suggested for functional diversity analysis (Pakeman & Quested, 2007), but it makes possible to keep all the species in the analysis (all of them are present in the analysed plots) and analyse a good percentage of the plots of the area (37%), distributed along the most part of the elevation gradient.

### *Null models*

In order to remove the effect of other factors that can affect community diversity (number of species and abundance structure), and be able to compare different communities, functional and phylogenetic diversity indices are standardized respect to a null hypothesis of independence between species identity (functional or phylogenetic) and species distribution (Kembel & Hubbel, 2006).

For a given community, standardized Rao index is calculated as follows:

$$std\ Rao = \frac{obs\ Rao - mean\ Rao(null)}{sd\ Rao(null)}$$

, where *obs Rao* is the observed value, *mean Rao* and *sd Rao* are respectively the mean and the standard deviation of the random distribution of Rao indices for that community under the null hypothesis.

The randomization is obtained by the permutation of rows and columns of the species distance matrix, while the abundances of species within the plots are kept unchanged. This kind of randomization is chosen because it is of simple interpretation, coherent with the correlation analysis, and has been demonstrated to be one of the best approaches to assess the significance of community metrics (Hardy, 2008). The randomization are done 1000 times.



The null hypothesis is rejected if the standardized Rao index falls into the critical region of 5% (p-value is not advisable as the Rao distribution all over the plots is not asymmetrical). The standardized Rao index of each plot is considered significantly high (low) if the observed value is higher than the 0.975 quantile (lower than the 0.025 quantile) of the null distribution of the plot.

A non-parametric Wilcoxon test is performed to test if the mean of the standardized Rao all over the plots is significantly different from 0 (a T test could not be used because the Rao distributions are not normal).

Functional and phylogenetic diversity are plotted against each other and their correlation is assessed with Spearman's correlation test, as the distributions are not normal.

### *Variation of community diversity along the elevation gradient*

Standardized Rao indices are plotted against plot elevation to assess if there is a pattern in community diversity respect to the main indirect gradient of the area. The significance is tested with a linear model approach, as the data do not follow a clear probability distribution and the deviation of the error distribution from the linear model hypothesis is not large.

In order to define elevation as the best environmental predictor, the predictive ability of the five topoclimatic variables was previously tested too, by using additive linear model and model simplification.

All the analysis is performed with R 2.10.1 (R Development Core Team 2010). The randomization codes are appositely written to optimize the analysis.

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## **GENERAL CONCLUSIONS**

### **Project 1: modelling eco-evolutionary dynamics of temperature dependent consumer-resource system**

The model shows that metabolic selective forces can drive consumer and resource body sizes into co-evolutionary arms races, i.e. the consumer body size tracks the resource body size. The relevance of these evolutionary changes decreases with the strength of the background stabilizing selection and increases with the strength of the consumer specialization on the size of the resource. According to the model, warming has a main effect on the evolution of the system, which is a rise of the speed and extent of evolutionary change, driven by an increase of the coefficient of selection with temperature. Moreover, according to the model, evolution can have different feedback effects on the ecological dynamics, either by preventing the system to shift from equilibrium dynamics to cycles or by enhancing consumer extinction. In particular, the second outcome, which occurs when the system is low-enriched (low resource carrying capacity) and the consumer thermal impact is negative (the death rate increases faster than the consumption rate with temperature), suggests that evolutionary change could in some cases contribute to destabilize high trophic levels.

### **Project 2: functional and phylogenetic structure of subalpine meadow plant communities**

The analysis detected clustering in the functional structure of the communities all over the study area, i.e. species sharing similar habitats tend to have traits more similar than expected by random processes of species distribution; this likely indicates that environmental filtering is relevant in determining the community assembly along the elevation gradient. The overall phylogenetic structure instead has been found to be not different from random, and the functional traits responsible of the functional structure are moderately labile – they display a phylogenetic signal but lower than expected by Brownian evolution. This suggests that convergent evolution of distant lineages on the same habitats played a role in shaping community composition. Finally, both functional

and phylogenetic diversity – which are anyhow related to each other in single plots – have been found to be lower at low elevation, suggesting a possible effect of anthropogenic land use - e.g. herbivores, pesticides, and higher disturbance regimes - in constraining community biodiversity.

## **General remarks**

The work explored two different and complementary research area and approaches to eco-evolutionary responses of communities to global change. Nevertheless, a general indication can be drawn from the two projects: evolution can play a relevant role in the response of biological communities to environmental change, both on short and long time scale and within and between trophic levels. The conditions that make evolution relevant and its feedback effects on the ecological properties still remain to be fully deepened, and in particular further work should be done to clarify how species interactions are involved in these processes. For instance, consumer-resource mechanistic models could be extended to multispecies food webs, in order to investigate if there is overall a stronger evolutionary mismatch between low and high trophic levels in systems that span more orders of magnitude. It also could be possible to investigate if – with more interacting species – the responses are more ecological (change of the trophic links between species) rather than evolutionary, as found within trophic levels (de Mazancourt et al., 2008). The analysis of the functional and phylogenetic structure of communities could instead be zoomed on similar communities and/or closely related species in order to look for limiting similarity among species that share similar habitats. Studying limiting similarity could be important both because it could be a driving force for colonization of new environmental niches, and on the other hand, it could prevent for adaptation in habitats where there are already competitors (Ackely, 2003).

Indications from such works can be useful to focus on main processes and factors important to understand community responses to environmental change, and eventually to incorporate them into models to predict future changes. For instance, metabolic models are particularly suitable for aquatic ecosystems, which can be composed of numerous overlapping trophic levels and are strongly structured by body size (Brose et al., 2006). Such modelling frameworks could also be used to investigate the interplay between climate change and other important anthropogenic pressures, like the overexploitation of fish resources, in affecting larger body sized and higher trophic levels (Daufresne et al., 2009). The analysis of community structure, instead, can be easily applied to terrestrial ecosystems, which strongly rely on the diversity of sessile long-living primary producers – the plants – insomuch as the Hearth's biotas are classified according

to them. In particular, the analysis of community structure could help in improving predictive niche models of future communities, which are based on niche similarity and on niche conservatism assumptions (Guisan & Thuiller, 2005; Ferrier & Guisan, 2006).

In general, merging different approaches can help in looking for new perspectives to face conservation and sustainability issues, which often require multidisciplinary contributes. In this context, evolutionary biology has a great potential in understanding the drivers of biodiversity, evaluating responses to human disturbance and the implications for ecological communities, ecosystems services, sustainability and biosecurity (Hendry et al., 2010). Hopefully, greater attention will be given in the future to these broader implications, to improve biodiversity science, conservation and policy (Hendry et al., 2010).

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## **Allegato: Riassunto in lingua italiana**

### **Contesto generale**

#### **Impatto antropico sugli ecosistemi**

La terra e i suoi ecosistemi stanno sperimentando rapide modificazioni su larga scala. Con l'aumento spropositato dello sfruttamento antropico dell'ambiente si prevede che l'impatto dei principali fattori responsabili del cambiamento ambientale globale – come i mutamenti climatici e la perdita e frammentazione degli habitat naturali – aumenterà significativamente in breve tempo (Tylianakis et al., 2008).

È stato ampiamente dimostrato che i cambiamenti climatici in atto sono in grado di influenzare la fenologia delle specie, producendo uno slittamento temporale di vari eventi primaverili del ciclo biologico delle specie, come l'apertura delle gemme, la fioritura, l'uscita dall'ibernazione, l'accoppiamento e la migrazione (Parmesan, 2006). In aggiunta, variazioni nell'abbondanza locale e slittamenti della distribuzione geografica delle specie verso maggiori latitudini e altitudini sono stati documentati in tutti i continenti e nella maggior parte dei principali oceani, sia per organismi vegetali che animali (Parmesan, 2006). Lo sfruttamento antropico dell'ambiente sta causando una massiccia perdita di habitat naturali, coinvolgendo molte specie appartenenti a diversi taxa (Owens & Bennet, 2000; Giam et al., 2010). Inoltre, l'antropizzazione del territorio favorisce la diffusione di specie invasive e l'omogeneizzazione della diversità biologica (Cassey, 2002). Non da ultimo, vari studi mostrano che diversi fattori che governano il cambiamento ambientale globale spesso agiscono in sinergia, riducendo ulteriormente la capacità complessiva delle specie di farvi fronte (Tylianakis et al., 2008).

#### **Interazioni tra specie e prospettiva di comunità**

Numerosi studi analizzano le risposte di singole specie al cambiamento ambientale globale, ma nei sistemi naturali le specie sono in relazione reciproca attraverso svariate interazioni sia negative (competizione, predazione, parassitismo) sia positive (mutualismo, facilitazione, impollinazione), che complicano le modalità di persistenza delle singole specie (Berg et al., 2009). La rottura delle interazioni entro le comunità biologiche, ad esempio nei sistemi preda-predatore o pianta-impollinatore, può insorgere dalla mancata corrispondenza tra le risposte delle diverse specie al mutamento ambientale, in particolare da discordanze nella sensibilità termica o nella capacità di

dispersione (Berg et al., 2009). Interazioni destabilizzanti, legate a nuovi patogeni o competitori, possono invece manifestarsi in seguito alla migrazione e alla diffusione di specie invasive (Tylianakis et al., 2008).

Inoltre, a livello di comunità, fattori ambientali e interazioni tra specie concorrono nel determinare la diversità biologica tra specie coesistenti: come già riconosciuto da Darwin, e in seguito sviluppato con la teoria della nicchia ecologica, se da un lato il comune filtro ambientale favorisce specie con caratteri ecologici simili, dall'altro le interazioni tra specie tendono a limitare la similarità tra specie coesistenti (Cavender-Bares et al., 2009). La diversità entro le comunità biologiche è una proprietà emergente fondamentale, poiché è in relazione con proprietà funzionali a livello di ecosistema, come la produttività, il riciclo dei nutrienti, il sequestro del carbonio atmosferico, e la resilienza al cambiamento ambientale (May & McLean, 2007). La biodiversità, infatti, dovrebbe promuovere la complementarità e incrementare il funzionamento degli ecosistemi, attraverso la massimizzazione dell'uso delle risorse; inoltre, essa dovrebbe assicurare la presenza di una varietà sufficiente di strategie ecologiche affinché il funzionamento dell'ecosistema persista in seguito a condizioni ambientali mutevoli (Cavender-Bares et al., 2009).

Quindi, semplicemente inferire le risposte di sistemi multi specie dalle risposte di singole specie può rivelarsi insufficiente e un approccio sistemico è auspicabile per capire come il cambiamento ambientale globale influenzi le comunità nel loro complesso (Berg et al., 2009) e in definitiva i beni e i servizi forniti dagli ecosistemi, sui quali è basato il benessere dell'uomo (Dobson et al., 2006).

### **Risposte ecologiche ed evolutive al cambiamento ambientale**

Le comunità biologiche possono rispondere al cambiamento ambientale attraverso risposte ecologiche, come slittamenti nella fenologia o nella distribuzione geografica e plasticità fenotipica di tratti ecologici, ma anche attraverso l'evoluzione adattativa (Parmesan, 2006; Kinnison & Hairston JR, 2007). Allo stato attuale, i processi ecologici ed evolutivi sono stati raramente studiati assieme in sistemi multi specie (de Mazancourt et al., 2008). Una sintesi emergente tra ecologia di comunità e biologia evoluzionistica sta però mostrando che i processi evolutivi su scala temporale lunga e breve possono influenzare la dinamica e la struttura delle comunità; allo stesso modo le interazioni ecologiche tra specie all'interno delle comunità possono influenzare processi micro e macro evolutivi (Johnson & Stinchcombe, 2007; Fussmann et al., 2007).

Su scala temporale breve, la genetica di popolazione può aiutare a comprendere la portata con la quale perturbazioni ambientali causate dall'uomo inducono una rapida evoluzione (su scala umana) (Kinnison & Nelson, 2007) e come il cambiamento evolutivo in tratti ecologicamente importanti può influenzare la dinamica delle comunità (Johnson & Stinchcombe, 2007). Studi su popolazioni naturali mostrano che cambiamenti a breve termine in tratti adattativi possono salvare popolazioni locali dall'estinzione (Kinnison & Nelson, 2007). Se l'evoluzione contemporanea sia sufficiente per mitigare gli effetti del cambiamento ambientale a livello di specie e di comunità è però oggetto di ampio dibattito (Parmesan, 2006). Risposte evolutive rapide possono anche comportare costi sul lungo termine, per esempio attraverso la perdita di diversità genetica (Rodriguez-Trelles & Rodriguez, 1998) o attraverso la selezione di tratti che compromettono il tasso di crescita della popolazione (Rankin & Lopez-Sepulcre, 2005; Orr & Unckless, 2008). In aggiunta, una mancata corrispondenza tra risposte evolutive di diverse specie, dovuta a differenti tassi evolutivi, può portare alla distruzione delle interazioni tra specie (Berg et al., 2009), per esempio in sistemi con livelli trofici multipli o in interazioni parassita-ospite.

Su scala temporale lunga, la ricostruzione filogenetica permette di investigare quanto i pattern di biodiversità attuali sono stati influenzati dall'interazione tra evoluzione e cambiamento ambientale nel passato. Per contro, questi studi possono aiutare a predire cosa possa accadere ai pattern di biodiversità in vista di futuri mutamenti ambientali (Hendry et al., 2010). Per esempio, la filogenesi può contribuire a comprendere come il cambiamento ambientale, in un contesto di comunità, sia in grado di produrre cambiamenti evolutivi nelle proprietà ecologiche delle specie e quindi influenzare l'assemblaggio delle comunità stesse. Il conservatorismo di nicchia, ovvero la tendenza delle specie e dei lignaggi a mantenere le proprie nicchie ecologiche invariate nel tempo, è stato ampiamente documentato in molteplici taxa; d'altro canto, anche la labilità di nicchia, ovvero la radiazione evolutiva delle nicchie ecologiche, è stata documentata (Pearman et al., 2007). Recenti meta-analisi suggeriscono che i processi ecologici, come l'inseguimento dell'habitat da parte delle specie, sono i fattori prevalenti nel determinare l'assemblaggio delle comunità in sistemi relativamente saturi di specie (Ackerly, 2003). La competizione interspecifica è stata indicata come una possibile causa di questo fenomeno, in quanto in grado di produrre selezione stabilizzante sulle specie appartenenti a comunità con un'alta diversità, inibendo quindi l'adattamento delle singole specie a nuovi habitat in presenza di competitori (de Mazancourt et al., 2008).

In sintesi, la portata e le condizioni nelle quali processi ecologici ed evolutivi concorrono, su breve e lunga scala temporale, nell'influenzare le dinamiche e i pattern delle comunità

non sono ancora del tutto chiariti (Johnson & Stinchcombe, 2007), ma vi sono crescenti evidenze del fatto che l'integrazione tra ecologia di comunità e biologia evolutiva potrebbe portare un contributo rilevante per comprendere il cambiamento ambientale globale in atto (Hendry et al., 2010).

## **Presentazione del lavoro di tesi**

Il contesto sopra delineato è stato esplorato nel corso di un anno di tirocinio, nell'ambito del Master di Ricerca in Ecologia, Evoluzione e Conservazione svolto presso l'Imperial College London, sotto la supervisione del professor Timothy Barraclough. Il lavoro ha incluso due mesi di lezioni introduttive e due progetti di ricerca di cinque mesi ciascuno.

Le lezioni hanno riguardato i seguenti argomenti: Ecologia di comunità delle piante e conservazione, Speciazione ed evoluzione della biodiversità, Modelli di dinamica di popolazione, Demografia e gestione delle popolazioni naturali, Conservazione globale della biodiversità e GIS, Ecologia del cambiamento climatico e funzionamento degli ecosistemi; Statistica con R; Corso avanzato in modelli di dinamica di popolazione e di ecologia di comunità con R.

I progetti esplorano due differenti aree di ricerca e diversi approcci matematici e statistici per lo studio delle risposte delle comunità biologiche al cambiamento ambientale, integrando aspetti ecologici ed evolutivi. Il primo progetto è stato effettuato presso l'Imperial College London e il secondo presso l'Università di Losanna (Svizzera), in qualità di *visitor student* dell'Imperial College. Ciascun progetto è stato scritto secondo lo stile di una specifica rivista scientifica (rispettivamente *Ecology Letters* e *Global Ecology and Biogeography*).

### **Primo progetto: modellizzazione della dinamica eco-evolutiva di un sistema consumatore-risorsa dipendente dalla temperatura**

Il primo progetto riguarda l'interazione tra dinamiche ecologiche ed evolutive su scala temporale breve. L'oggetto di studio è un sistema consumatore-risorsa, quindi l'attenzione è posta sulle interazioni tra livelli trofici. Il progetto studia gli effetti della temperatura, come variabile ambientale, sulla taglia degli organismi, come tratto soggetto ad evoluzione. Il meccanismo studiato è basato sulla dipendenza dei tassi metabolici – e quindi del flusso di energia attraverso la rete trofica – dalla taglia degli organismi e dalla temperatura. L'approccio è basato su un modello meccanico di dinamica

di popolazione del tipo Lotka-Volterra (Vasseur & McCann, 2005) basato sulla teoria dell'ecologia metabolica (Savage et al., 2004), integrato con un modello di genetica di tratti quantitativi (Iwasa et al., 1991), ed investigato tramite simulazioni.

### **Secondo progetto: struttura funzionale e filogenetica delle comunità di piante dei prati subalpini**

Il secondo progetto riguarda l'interazione su scala temporale lunga tra processi ecologici di nicchia e processi evolutivi, che concorrono nel determinare la struttura delle comunità. L'oggetto di studio è una serie di comunità naturali di piante localizzate nei prati delle Prealpi svizzere, quindi l'attenzione è posta sulle interazioni all'interno di uno stesso livello trofico. Il progetto analizza il ruolo del principale gradiente ambientale dell'area, rappresentato dall'altitudine, nel determinare la diversità funzionale e filogenetica delle comunità di piante. L'approccio è basato sull'analisi statistica della struttura funzionale e filogenetica delle comunità, ottenuta combinando i due principali metodi complementari utilizzati correntemente in letteratura, basati rispettivamente su correlazioni tra diversi tipi di dissimilarità tra coppie di specie (funzionale, filogenetica e di nicchia) e su metriche per la misura della diversità funzionale o filogenetica complessiva entro comunità (Vamosi et al., 2009; Cavender-Bares et al., 2009).

## **Conclusioni generali**

### **Primo progetto: modellizzazione della dinamica eco-evolutiva di un sistema consumatore-risorsa dipendente dalla temperatura**

Il modello mostra che le forze selettive legate ai processi metabolici possono guidare consumatore e risorsa in una corsa agli armamenti coevolutiva, in cui la taglia del consumatore segue i cambiamenti della taglia della risorsa. La rilevanza di tali cambiamenti evolutivi diminuisce con l'intensità della selezione stabilizzante di sottofondo e aumenta con l'intensità della specializzazione del consumatore sulla taglia della risorsa. Secondo il modello, l'aumento della temperatura ha un principale effetto sull'evoluzione del sistema, che consiste nell'aumento della velocità e della portata del cambiamento evolutivo, dovuto ad un incremento del coefficiente di selezione con la temperatura. Inoltre, il modello suggerisce che l'evoluzione può avere differenti effetti sulla dinamica ecologica, può infatti prevenire il sistema dal passare da una dinamica di equilibrio ad una instabile (ciclica), oppure favorire l'estinzione del consumatore. In particolare, il secondo effetto, che avviene quando il sistema è scarsamente arricchito (bassa capacità



portante della risorsa) e l'impatto termico sul consumatore è negativo (il suo tasso di mortalità aumenta più velocemente del tasso di consumo della risorsa, all'aumentare della temperatura), suggerisce che il cambiamento evolutivo potrebbe in alcuni casi contribuire alla destabilizzazione dei livelli trofici più elevati.

### **Secondo progetto: struttura funzionale e filogenetica delle comunità di piante dei prati subalpini**

L'analisi ha individuato la presenza di aggregazione nella struttura funzionale delle comunità studiate, cioè specie che condividono habitat simili tendono ad avere tratti più simili di quanto atteso da processi casuali di distribuzione delle specie; questo risultato sembra confermare che il filtro ambientale sia rilevante nel determinare l'assemblaggio delle comunità lungo il gradiente di altitudine. La struttura filogenetica complessiva è invece risultata non differente da quanto atteso da processi casuali, e i tratti funzionali responsabili della struttura funzionale sono risultati moderatamente labili – essi mostrano un segnale filogenetico, ma più basso di quanto atteso da un modello Browniano di evoluzione. Ciò suggerisce che l'evoluzione convergente di diverse linee evolutive sugli stessi habitat abbia avuto un ruolo nel determinare la composizione attuale delle comunità. Infine, sia la diversità funzionale che filogenetica, che sono ad ogni modo correlate nelle singole comunità, sono state trovate minori a bassa altitudine, suggerendo un possibile effetto di fattori legati all'uso antropico del territorio - quali il pascolo di animali da allevamento, l'uso di pesticidi ed elevati regimi di disturbo - nel limitare la biodiversità delle comunità di piante.

### **Considerazioni complessive**

Il lavoro ha esplorato aree di ricerca e approcci complementari per lo studio delle risposte eco-evolutive delle comunità al cambiamento ambientale globale. Un'indicazione generale può essere tratta dai due progetti: i processi evolutivi possono avere un ruolo rilevante nella risposta delle comunità biologiche al mutamento ambientale, sia su scala temporale breve che lunga e sia all'interno che tra livelli trofici. Le condizioni che rendono tali processi evolutivi rilevanti, così come i loro effetti sulle proprietà ecologiche, restano ancora da approfondire, ed in particolare ulteriori ricerche dovrebbero essere svolte per chiarire come le interazioni tra specie siano coinvolte in questi processi. Per esempio, modelli dinamici del sistema consumatore-risorsa potrebbero essere estesi a reti trofiche multi specie, in modo da investigare se sistemi che coprono diversi ordini di grandezza mostrano una discordanza maggiore tra risposte evolutive dei livelli trofici basali e apicali. Potrebbe anche essere possibile indagare se – in presenza di più specie interagenti – le

risposte siano prevalentemente ecologiche (cambiamento nelle relazioni trofiche tra specie) piuttosto che evolutive, così come è già stato trovato all'interno di uno stesso livello trofico (de Mazancourt et al., 2008). L'analisi della struttura funzionale e filogenetica delle comunità potrebbe invece essere focalizzata su comunità simili e/o specie strettamente imparentate in modo da poter investigare la presenza di un limite alla similarità tra specie che occupano lo stesso habitat. Includere tale analisi potrebbe essere importante perché un limite alla similarità tra specie coesistenti potrebbe sia favorire la colonizzazione di nuovi habitat, sia inibire l'adattamento in habitat dove già sono presenti competitori (Ackerly, 2003).

Indicazioni ottenibili da simili lavori potrebbero essere utili per individuare i principali processi e fattori coinvolti nelle risposte delle comunità al cambiamento ambientale ed eventualmente migliorare gli strumenti predittivi. Per esempio, i modelli metabolici sono particolarmente adatti a ecosistemi acquatici, che possono essere composti di numerosi livelli trofici sovrapposti e sono fortemente strutturati in base alla taglia degli organismi (Brose et al., 2006). Tale tipologia di modelli potrebbe anche essere utilizzata per indagare l'interazione tra cambiamento climatico e un'altra importante pressione selettiva antropica, lo sfruttamento delle risorse ittiche, nello sfavorire i pesci di grossa taglia (Daufresne et al., 2009). L'analisi della struttura delle comunità biologiche, invece, può essere facilmente applicata agli ecosistemi terrestri, fortemente basati sulla diversità di produttori primari sessili e con lunghi tempi generazionali – le piante – (Brose et al., 2006), a tal punto che i biomi terrestri sono classificati in relazione ad essi. In particolare, lo studio della struttura delle comunità potrebbe contribuire a migliorare i modelli predittivi della composizione delle comunità, che sono basati sulla similarità tra nicchie delle specie e su assunti di conservatorismo della nicchia (Guisan & Thuiller, 2005; Ferrier & Guisan, 2006).

Più in generale, combinare differenti approcci può contribuire a identificare nuove prospettive per affrontare questioni in ambito di conservazione e sostenibilità, che per la loro natura complessa spesso richiedono contributi multidisciplinari. In questo contesto, la biologia evolutiva ha un grande potenziale per comprendere i fattori che influenzano la biodiversità, studiare le risposte evolutive all'impatto antropico e valutare le implicazioni per le comunità ecologiche, per il funzionamento degli ecosistemi e per la sostenibilità (Hendry et al., 2010). Si auspica quindi che una maggiore attenzione sia data in futuro a queste ampie implicazioni, nell'ottica di apportare contributi allo studio della biodiversità, alla sua conservazione e ad una più ampia riflessione sugli aspetti sociali e politici che vi sono inestricabilmente legati (Hendry et al., 2010).