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Research Article

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Positive Niche Construction: Incorporating Facilitative Microhabitat into Mechanistic Niche Modeling

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Abstract

Researchers in the fields of conservation biology and invasion ecology aim to predict the dispersal of species in a reproducible manner, based on quantifiable relationships between target organisms and their environment, through a process known as mechanistic niche modelling. By identifying physiological constraints unique to an organism and calculating its budget of key resources in a given location, sophisticated estimates of potential activity and fecundity can be developed. These spatially-dependent dynamic energy budgets (DEBs) currently ignore the general phenomenon of biological facilitation and, in particular, positive niche construction, wherein a single species improves the suitability of their local habitat for future individuals by modifying their own microclimate. From bed-forming mussels to canopy-forming trees, diverse species can modify their own microclimates by increasing habitat complexity and, in doing so, ameliorate the same physical stressors explicitly considered in mechanistic niche models. To demonstrate the applicability of facilitative habitat in these models, this study selects two habitat-forming organisms and employs DEB-based hindcasting tools to simulate (1) the growth and allocation impacts of temperature regulation in *Mytilus edulis* (blue mussel) beds and (2) the near-ground micrometeorological impacts of *Fagus* (beech) tree canopy coverage. A significant reduction in growth and reproductive capacity in blue mussels beyond their optimal temperature and an overall amelioration of temperature and water stress below the beech canopy were observed. Although further research is required to refine the microclimate and micrometeorological impacts assumed for these model organisms, these results suggest that maturing around conspecifics can facilitate persistence in otherwise poor quality habitat. Thus, both species are predicted to have a significant Allee niche, demonstrating the need to incorporate facilitative habitat into mechanistic niche models, especially those used to predict climate change-induced range shifts.

Introduction

Part 1: Microhabitat Regulation by Blue Mussels

Because vegetative growth increases the vertical and horizontal structural complexity of landscapes, nearly all vegetation-dominated habitats (forests, marshes, etc.) can be considered biogenic[1]. In marine ecosystems, these facilitated environments can be critical for the growth of diverse species, e.g. juvenile fish preferentially inhabit bryozoan beds[2]. Biogenic habitats often harbor complex ecosystems characterized by high biodiversity[3], in part due to organisms experiencing reduced physical stress through the physically-ameliorating traits of structure-forming species[1], whose facilitation of other species is often a byproduct of their normal activity[2]. For example, canopy trees in dense forests insulate the subcanopy from temperature extremes and increase subcanopy humidity by evapotranspiring and retaining water in their own biomass and in the soil below[1]. Even small forest plants, like subcanopy shrubs and bracken, can reduce summertime soil temperatures and increase water availability[1]. Meanwhile, in intertidal zones, aggregated seaweeds and invertebrates form beds that protect species below this "canopy" from heat and desiccation[1]. Beds of sessile mussels can reduce peak temperatures in their immediate microclimate by 20 °C. This is a functional trait that can combat the thermal stress characteristic of non-optimal climate latitudes, leading to unexpected persistence patterns for resident species[1]. Mussels themselves also alter water clarity and sediment chemistry by filter feeding[2], further influencing the environment and thus evolutionary pressures experienced by local species.

Microclimate modifications like this can complicate assessments of invasion potential. Along the South African intertidal, for example, the indigenous mussel and ectotherm *Perna perna* periodically opens its shell to aerobically respire[4]. While this behavior results in no body temperature effects in solitary mussels, in aggregate beds of conspecifics, researchers have observed evaporative cooling, leading to decreased group body temperatures and thus reduced desiccation and heat stress[4]. The invasive mussel *Mytilus galloprovincialis* does not exhibit this behavior but has managed to successfully invade the southern coast of South Africa, despite desiccation pressures[4]. After researchers manipulated the densities of native *Perna perna* and invasive *M. galloprovincialis* mussels in intertidal beds along this coast, they found that both the native and invasive mussel benefitted from group evaporative cooling facilitated by *Perna perna*[4]. Thus, the persistence of *M. galloprovincialis* outside its native range may be enabled by the thermoregulating presence of *Perna perna*, highlighting the need to consider stress-ameliorated habitat in predicting the limits of invasion by *M. galloprovincialis*[4].

Although obligate associations, i.e., interspecific relationships required for the persistence of at least one partner between habitat-forming species and resident heterospecifics (other species), are more common in tropical systems[3], these associations remain ecologically important in Canada and support the productivity of many fisheries[2]. Marine mussels like *Mytilus edulis* (blue mussel) can provide complex structure to marine substrate as a single species by producing byssus threads. Assemblages of organisms can also build biogenic habitat[2]. Thus, understanding the natural population dynamics of species residing in facilitative habitat and assessing the net impact of human activities on this regime requires knowledge of numerous supporting species[2].

Loss of quality habitat caused by anthropogenic climate change disproportionately threatens freshwater and coastal organisms and compounds other anthropogenic stressors, leading to accelerated biodiversity loss[2]. For example, climate change exacerbates the heat and desiccation stresses characteristic of the rocky intertidal[1]. However, one investigation of warming impacts on mussel bed inhabitants in the Bodega Marine Reserve observed a strong decoupling of microhabitat conditions from external climate variation. The study found no significant relation between simulated hot-dry climate change scenario and frequency of lethal desiccation in isopods and crabs, despite evidence for mortality in these species being closely associated with co-occurrent desiccation and thermal stress outside this buffered habitat[1]. The reliance of these species on mussel beds poses an indirect, unique vulnerability to climate change, however, as biogenic habitats often exhibit very slow recovery times[3]. The stress response of these taxa may therefore be characterized by a tipping point, up until which the mortality of buffered species may be unaffected until the engineering species itself is sufficiently stressed to cause the breakdown of the facilitative habitat and with it, the facilitated community[1].

The strength and prevalence of microclimate manipulation abilities in structure-forming species suggests that estimations of current and future distributions of these species and local residents must consider the hysteresis of habitat suitability, as potentially lethal macroclimatic conditions may conceal the presence of a nonlethal microclimate[1]. The uncertainty and potential lethality of climate change for myriad species and biogenic habitats themselves justifies studying microclimate-modifying species and the dynamics of physical facilitation[1]. Likewise, the recent acceleration of global biological invasions demands better predictions of the invasion potential for these habitat-forming species and their facilitated heterospecifics[1].

To estimate current habitat suitability and predict future range shifts, ecologists have turned to mechanistic niche modelling. This class of methods relies on ecophysiological data, such as target species-specific minimum/maximum temperature tolerances. They reduce the global landscape of climatic variation down into patches where the resource needs and environmental constraints of the target species are satisfied, thus identifying its potential distribution[5]. While these models generate more explanatory predictions of persistence than their correlative counterparts, they intrinsically neglect some aspects of the target species' biology, including dispersal ability, behavior, competitive fitness, and genetics. Additionally, many target species effectively persist in facilitative habitats, meaning that mechanistic niche models based on individual species' traits will fail to recognize the spatial boundaries of all quality biogenic habitat[1]. Their strict focus on the physiology and behavior of a target species overestimates the importance of these parameters, as the population dynamics and dispersal of a given species may be altogether controlled by a facilitating, microclimate-modifying counterpart[1].

Mechanistic niche models can employ Dynamic Energy Budgets (DEBs) to estimate the ability of a species to persist within a physiologically relevant set of climate conditions by calculating the net resource surplus accessible to the organism given its allocation needs, activity costs, and resource availability[5]. Building a dynamic energy budget for a target species requires estimating various metrics, called DEB parameters, of that organism's allocation strategy, reproductive costs, respiration costs, nutritional needs, and climate tolerances. To expand the biological traits considered in traditional DEB-based mechanistic niche modelling and to quantify the impact of conspecific habitat facilitation, also called positive niche construction, I here select *Mytilus edulis* (blue mussel) as a target species known to facilitate microhabitat by reducing local thermal stress[6]. I then compare its predicted persistence ability with and without the ameliorating influence of a conspecific mussel bed at a specific site in its native range.

Part 2: Micrometeorology Below Beech Trees

Key metrics of microclimate, including solar radiation, air and soil temperature, water availability, and wind, are significantly modified by forest vegetation. This leads to distinct microclimate profiles along vegetation type and land use axes[7]. Simultaneously, local plants adapt to ambient microclimatic conditions, e.g. air temperature controls respiration, water transport, and soil formation rates[8]. This simultaneous feedback between forest plants and their immediate microclimate creates an ecological system where the dynamics of individual elements are mutually dependent[7].

The heterogeneous microclimate landscape within forests leads to characteristically high subcanopy biodiversity, as the competitive fitness of individual plant species changes with the environmental conditions they experience at an organismal scale[8]. For example, light availability alone influences seed germination, recruitment, and establishment[9]. Forest plants also respond to microclimatic variation physiologically, e.g. beech trees exhibit reduced water uptake, root growth, foliage mass, and radial growth with lower wintertime soil temperatures[8]. Across taxa, branches adapt architecturally to light availability, and the inclination angle of leaves themselves reflects available solar radiation[7]. Throughout maturation, the relative abundance of sun and shade optimized leaves also changes depending on light availability[7].

Concurrently, forest plants, especially canopy trees, significantly modify the microclimate experienced by other forest residents[10]. Below the canopy, species experience lower maximum temperatures, higher minimum temperatures, and higher humidity[11]. This suggests that large trees moderate annual and seasonal climatic variation below the canopy, leading to a habitat with ameliorated physical stress conditions[11]. Overstory foliage further regulates the transmittance of light–that is, the amount that reaches the understory[9]. Canopy composition can also affect this quantity, as species-specific porosity, height, and spacing all impact the transmittance, quality, and variability of understory light[9,11]. Structural properties of these canopy species, such as leaf area index (LAI) and leaf distribution[7], can be used to calculate light transmittance according to Beer-Lambert's Law[9,11]. All forest management activities that adjust crown structure, canopy openness, and community composition thereby affect the amount of solar radiation available in the subcanopy[7,11]. This microclimate parameter regulates understory plant diversity, productivity, and competitive dynamics[12], and thus, controls on this parameter have ecosystem-wide consequences.

Overall, forest vegetation reduces local wind speed, depending on the size and distribution of plant biomass[7]. However, gaps in the canopy can generate turbulence and increase the prevalence of small turbulent eddies[7]. This explains the intentional placement of meteorological weather stations in wide clearings to better represent regional rather than localized conditions[13]. Furthermore, because of high evapotranspiration rates in forests, relative humidity is greater below forest canopies than above clearings[7].

Although the temperature profile within a forest varies throughout the day and year, in general, the presence of forest species reduces daily and seasonal temperature variation when compared to open ground, i.e. soils below a developed canopy exhibit warmer winter temperatures and colder summer temperatures than their exposed counterparts[7]. Soil temperature has remained an understudied aspect of microclimate despite being shown to significantly affect the photosynthesis, respiration, and growth of forest species[7]. However, in forestry, the importance of this sheltering phenomenon in stand growth and recruitment has already been established[7]. Microclimate impacts of dense forest cover can even be seen in adjacent disturbed patches, in a phenomenon known as "forest influence"[14]. The reduced dispersal distance and physical amelioration of this adjacency effect can lead to faster recolonization of disturbed patches by mature forest communities[14]. This explains the increasingly common silvicultural practice of retention forestry, wherein mature patches are left within harvested areas to accelerate regeneration and, incidentally, recover biodiversity[14].

While these sheltered environments ameliorate some climatic stresses like drought and wind throw, the net impact of forest cover on recruitment is not linear, as many seedlings respond best to partial thinning of forest cover achieved via disturbance or harvesting[14]. In silviculture, juvenile growth appears optimized at canopy coverages between 25% and 75% depending on the ecophysiology of the cultivar[7]. This growth preference likely stems from the combined effects of reduced resource competition and remnant forest influence. The nontrivial dynamics of forest influence demonstrate the complexity of assessing growth conditions at a given stand density.

Despite the uncertainty regarding subcanopy light availability and thus growth suitability, the positive impact of forestation on temperature and humidity demonstrates the ability of forest cover to insulate the subcanopy environment from macroclimatic variation[15]. At local scales, this temperature buffering capacity depends on the thermodynamic efficiency of the ecosystem, as forest stands with a more homogenous distribution of biomass (e.g., a plantation) absorb and dissipate solar radiation more efficiently than stands structured heterogeneously (e.g., a mature, naturally regenerating forest)[11]. Accordingly, the amount of litter in a forest habitat affects its thermodynamic efficiency, soil evaporation rate, water retention capacity, and thus macroclimate buffering capacity[11]. It follows that to build accurate heat and dynamic energy budgets for resident species, researchers must study the thermodynamic efficiency of forest ecosystems[11]. Furthermore, this quantity reflects the ability of an ecosystem to buffer broader scale global warming and with it, thermophilization, or phase shifts towards species better adapted to higher temperatures[11].

One assessment of plant community thermophilization relied on correlative niche modelling to calculate the history of floristic temperature at resurveyed vegetation plots in North America and Europe based on their unique community assemblages[15]. The authors observed a higher frequency of warm-adapted understory plant species with time. This thermophilization occurred more rapidly in areas with higher warming rates[15]. In forests that became denser over the study period, thermophilization occurred more slowly, suggesting that the closure of temperate forests has historically insulated understory plant communities from macroclimatic warming and slowed associated phase shifts[15]. In another study that compared the microclimate-buffering capacities of primary and secondary forests, plantation forests exhibited $< 2.5\ ^\circ$C hotter understories than their old growth counterparts, which were characterized by higher biomass throughout various vegetation levels[13]. Overall, this significantly greater ability of old-growth forests to buffer macroclimatic change, even at similar canopy densities, demonstrates the need to critically examine management practices[13]. Such examination is essential if stakeholders are to leverage habitat facilitation to slow biodiversity loss in complex ecosystems.

Forests' ability to ameliorate subcanopy stress and thus facilitate viable microhabitat invites the challenge of incorporating this facilitation into contemporary mechanistic niche models to improve our estimates of current and future biogeography. One way to acknowledge this phenomenon is to estimate the temperature impacts of a particular canopy species on the understory and identify changes to the suitability of that facilitated microhabitat. In light of its disproportionately severe reduction of near-ground solar radiation at a given canopy coverage, this study uses the genus *Fagus* (beech) to analyze the near-ground micrometeorological effects of tree coverage[11]. It has been shown that subcanopy solar radiation significantly affects beech recruitment by affecting LAI growth, mainly during early growth stages[12]. Thus, by comparing the influences of canopy coverage and macroclimatic warming on the microclimate experienced by juvenile beech trees, the importance of positive niche construction to this canopy species can be estimated.

Methods

Part 1: Microhabitat Regulation by Blue Mussels

To simulate the effect of increased body temperature on various life history, allocation, and growth parameters in blue mussels, I used the Dynamic Energy Budget Model in the Sea (Kearney & Porter[5]), one of the Biological Forecasting and Hindcasting Tools developed by Professor Michael Kearney's group at the University of Melbourne. This tool relies on the DEB modelling function built into NicheMapR, an R package developed by that same group to simulate microclimate conditions and thus produce mechanistic niche models of endothermic and exothermic organisms[5]. Calculations of blue mussel ecophysiology (growth, weight, reproduction, oxygen consumption, etc.) under modeled conditions thus derive from a mass budget scheme which can be described by stoichiometric equations of the standard model of Dynamic Energy Budget theory (see Supplementary Figure 5). This function is informed by DEB parameters sourced from the Add-my-Pet (AmP) collection, a self-described open-access scientific journal to which researchers contribute their findings on animal species-specific energetics, including DEB parameters, and their methods for deriving these quantities and associated species traits[16].

The DEB Model in the Sea hindcasting tool utilizes sea surface temperature data provided by the National Oceanic and Atmospheric Administration (NOAA) (Kearney & Porter[5]). Species-specific DEB parameters (z – size multiplier, κ – allocation fraction of growth and somatic maintenance, and Tb – body temperature) are input by the user with the model conditions (initial stage, ageing, post-hatch respiration, location). Having collated the required DEB parameters from various sources[16–21] (z, κ, and Tb for the DEB Model in the Sea, see Supplementary Figure 4), I analyzed the (1) total wet mass gain, (2) change in reproduction buffer, and (3) onset of puberty in maturing blue mussels initially at the egg stage. The 365-day simulations occurred from January 31, 2020, to January 31, 2021, at coordinates 60° N, 1° E. Mussels were subject to initial body temperatures of 18, 20, 22, 24, 26, 28, and 30 $^\circ$C (see Supplementary Figure 1 for an example of parameter input). The output allocation and growth graphs were then visually analyzed for puberty onset, reproductive buffer, and wet mass gain.

Part 2: Micrometeorology Below Beech Trees

To identify the season- and temperature-specific subcanopy micrometeorological effects of preexisting beech dominance within temperate deciduous forest stands, I used another Biological Forecasting and Hindcasting Tool developed by Professor Kearney's group, the Global Soil Microclimate Calculator (Kearney & Porter[5]). For calculations of microclimate conditions (air temperature, humidity, wind speed, and solar radiation), this tool relies on the microclimate model built into NicheMapR, which is itself informed about surface climate by the 1960-1990 global climate grids produced by New et al.[5] The NicheMapR microclimate model consists of a Fortran library, the main calculation engine, and an assisting set of R functions that establish data inputs and call the Fortran program. For further information on the Fortran library, user inputs, and R outputs, see Supplementary Figure 6.

To simulate the impact of beech tree presence on otherwise bare soil in the Global Soil Microclimate Calculator, I manipulated the following terrain and soil parameters which would be most affected by the density of conspecifics in a beech stand: (1) percent shade (2) wind multiplier, and (2) percent albedo. I generated two sets of micrometeorological predictions based on two treatment regimes of these parameters corresponding to trees-present and bare soil terrain conditions based on the projected impacts of beech forestation throughout the year[7,8,13]. See Supplementary Figure 2 for an example of parameter input and Supplementary Figure 3 for an example of simulation output. I repeated treatments of tree presence and absence for simulations conducted in January and June, with and without a $2\ ^\circ\mathrm{C}$ climate offset to incorporate seasonal variation and compare the impact of beech tree subcanopy micrometeorology effects with and without macroclimatic warming. A location of $(42^\circ$ N, -79° E), roughly within Allegheny National Forest in the northeastern United States, was used across treatments.

Results

Part 1: Microhabitat Regulation by Blue Mussels

In the maturing juvenile blue mussels subject to a 365-day growth simulation, a distinct delay of puberty and eventual total inhibition of full maturation can be observed with increasing sustained body temperature treatments (Figure 1). Along this same axis of change, a reduction in final wet mass of 99.05% can be noted between $18\ ^\circ\mathrm{C}$ and $30\ ^\circ\mathrm{C}$ treatments (Figure 1). Likewise, the proportionally small reproductive buffer (top allocation layer present after puberty) ultimately vanishes with increasing body temperature, as puberty is delayed from day $\sim$110 to $\sim$270 until it is fully inhibited by $Tb = 28\ ^\circ\mathrm{C}$ (Figure 1).

Part 2: Micrometeorology Below Beech Trees

The effect of beech tree presence on surface micrometeorology depends on season and climate offset. In the January treatment without a climate offset, the presence of trees did not affect minimum soil temperature, minimum air temperatures, minimum humidity, or maximum solar radiation (Table 1). However, with $2\ ^\circ\mathrm{C}$ of warming, tree presence decreased minimum soil temperatures from $0\ ^\circ\mathrm{C}$ to $-3\ ^\circ\mathrm{C}$ (Table 1). Regardless of the warming offset, winter tree presence decreased maximum wind speed by 25% (Table 1). In the June simulation, tree presence was not associated with any changes in maximum solar radiation (Table 1). It was associated with a 24-25% reduction in maximum air temperature, depending on the warming scenario 1. Regardless of warming offset, the presence of trees in June increased minimum humidity from 30% to 45%, reduced maximum wind speed by 38%, and reduced maximum soil temperature by 41% (Table 1).

Discussion

Part 1: Microhabitat Regulation by Blue Mussels

The dramatic reduction in total growth, delay of puberty, and loss of the reproduction buffer observed in here in blue mussels with simulated heating from $18\ ^\circ\mathrm{C}$ to $30\ ^\circ\mathrm{C}$ reflects their posited ideal body temperature of $16\ ^\circ\mathrm{C}$ (ref. 17) and their upper limit of temperature tolerance, $23\ ^\circ\mathrm{C}$ (refs. 16, 17, 20). That being said, the loss of fitness observed here in simulated blue mussels subject to higher temperatures does not necessarily indicate that temperature amelioration will always lead to improved population-level fitness. This is due to the possibility of other ecological constraints (e.g., predation, competition, etc.) not considered in this single species DEB-based niche model potentially constraining the niche of this species more than thermal stress.

However, if this simulation of sustained body temperatures reflects the potential difference in growth and reproductive outcomes between mussels that mature on developed conspecific beds and those that settle on alternative substrates, then it evidences the theoretical positive niche construction ability of blue mussels, wherein the habitat modification performed by small invasive populations may facilitate the niche requirements of future individuals in otherwise unviable habitat[22]. If so, the hypothetical distribution of blue mussels becomes complicated by the existence of an Allee niche. This refers to the region of niche space in which there is a positive association between individual blue mussel fitness and population size[22]. Over time, if populations of blue mussels that settle on cooler developed conspecific beds continue to benefit from this Allee effect, then their invasion of previously unviable habitat may be accelerated following the survival of potentially few pioneering individuals that ameliorate conditions for following conspecifics. As studies have found contemporary ecophysiological models for blue mussels underestimate the spatial extent of their growth when compared to field observations[16], the current framework for mechanistic niche modelling of imposing physiological constraints on target species may systematically underestimate the true extent of habitat potentially suitable to these organisms by ignoring the facilitative microhabitat refugia identified here.

However, to validate the potential existence and longevity of an Allee niche for blue mussels, future research should compare the magnitude of positive, temperature ameliorating, and negative, density-dependent effects (e.g. intraspecific competition, decreased water flow) experienced by mussels living alongside conspecifics. If growth and reproductive outcomes remain higher for mussels on conspecific beds than for lone individuals, then further support would be found for net positive intraspecific interactions and positive niche construction. Conversely, if resource competition and overcrowding within mussel beds are found to limit mussel growth and fecundity in beds still subject to temperature amelioration across various carrying capacities, then positive niche construction, supported in this study, may prove insignificant to the persistence of mussels in the long term due to dominating negative intraspecific interactions.

Part 2: Micrometeorology Below Beech Trees

The summertime effect of beech tree presence on the simulation site can be summarized as an amelioration of hot and dry conditions below the canopy, wherein minimum humidity increased and the maximum temperature of both air and soil decreased. This phenomenon reflects the documented ability of beech stands and forests to generally increase local water availability by increasing the residence time of precipitation stored in biomass and continuously evapotranspiring[1]. Similarly, the significant additional shade provided by a largely closed beech canopy ($\sim$85%) reduces the amount of solar radiation reaching the subcanopy and surface, explaining the reduced maximum temperatures observed here.

The micrometeorological effects of tree presence in January reflect the loss of structural complexity caused by seasonal defoliation. With near-total canopy opening and thus minimal impedance of solar radiation, subcanopy air temperature was not impacted. Likewise, the domination of deciduous trees in this forest would lead to dramatically reduced evapotranspiration during this season, explaining the absence of humidity gains with trees present. The slightly reduced minimum soil temperature observed in forested sites provides an interesting insight into the nontrivial response of soil temperature to the presence of standing stock. Under high snow conditions ($0\ ^\circ\mathrm{C}$ offset), no temperature below $0\ ^\circ\mathrm{C}$ is recorded. This is likely due to the insulating effect of this snow layer. However, with $2\ ^\circ\mathrm{C}$ warming, the reduced snow layer may partially vanish near pockets of warmed vegetation, allowing the exposed soil below to be cooled below freezing later on by convection. Thus, the influence of standing stock on soil temperatures may depend on the abundance of other insulating cover, including snow.

The reduced maximum wind speed observed at forested sites in both June and January may be explained by the documented ability of beech stands to increase friction in the boundary layer and dissipate wind below the

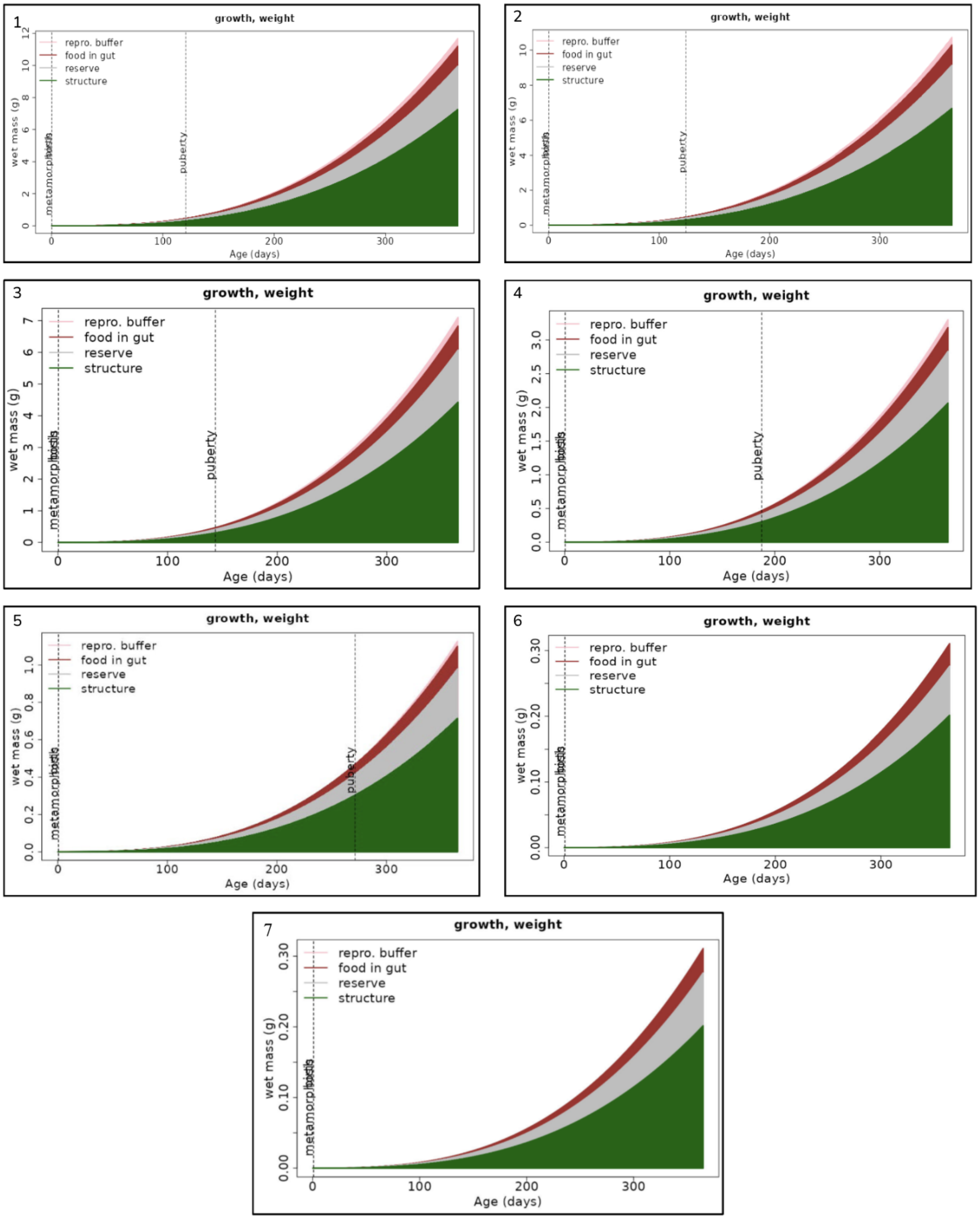

Figure 1. Panels 1-7 correspond to the simulated growth and biomass allocation outputs of DEB in the Sea (Kearney & Porter[5]) simulations for maturing blue mussels at constant body temperatures (1: $Tb = 18$ °C, 2: $Tb = 20$ °C, 3: $Tb = 22$ °C, 4: $Tb = 22$ °C, 5: $Tb = 26$ °C, 6: $Tb = 28$ °C, 7: $Tb = 30$ °C). Note the first dashed line corresponds to birth and immediate metamorphosis, while the second marks the onset of puberty. Parameters of simulation: Location = (54,3), Days = 365, Time step = hourly, Start date = Jan 31, 2020 at 1PM, $z = 4.2$, and $\kappa = 0.95$.

canopy[7]. However, when beech trees evapotranspire, they contribute to a super-subcanopy air density gradient which can create a vertical wind profile[7]. Therefore, the consistency of the forestation effect on maximum wind speed across seasons in these simulations may demonstrate that the physical structure of beech-dominated stands more significantly affects surface layer winds than their seasonally fluctuating evapotranspiring behavior does. The lack of changes in maximum solar radiation across all treatments may be explained by the assumedly incomplete closure of the beech canopy, which is characteristic of non-climax communities and results in gaps through which maximum solar radiation may reach lower vegetation levels. The overall greater amelioration of physical stressors by tree presence in the summer months agrees with the maximal strength of forest influence being recorded during this season[14].

The patterns in micrometeorology that emerge from these simulations of beech stand presence or absence can be used to analyze the comparative impact of cooling or warming and reforestation on surface conditions. Assuming the local terrain and soil property regimes compared in these

Table 1. Table of micrometeorological variables. Derived from the Global Soil Microclimate Calculator (Kearney & Porter[5]), these variables describe sites exhibiting terrain and soil parameters characteristic of bare surface or beech trees present. Outputs reflect daily average conditions below the canopy simulated in June (orange) or January (blue) with and without a +2 °C warming offset. Highlighted green values in Forestation Effect columns reflect notable variation in micrometeorology after the addition of trees to bare sites.

Micrometeorology	Bare Soil	Trees Present	Forestation Effect	Forestation effect (% difference)	Bare Soil +2 °C	Trees Present + 2 °C	Forestation Effect + 2 °C	Forestation effect (% difference)	Month
Max Ts (°C)	44	26	**-18**	**-41%**	46	27	-19	**-41%**	**June**
Max Ta (°C)	32	24	**-8**	**-25%**	34	26	-8	**-24%**	
Max Wind Speed (m/s)	0.8	0.5	**-0.3**	**-38%**	0.8	0.5	-0.3	**-38%**	
Max Solar Rad (W/m^2)	600	600	0	0	600	600	0	0	
Min Humidity (%)	30	45	**15**	**50%**	30	45	**15**	**50%**	
Min Ts (°C)	0	0	0	0	0	-3	**-3**	**undefined**	**January**
Min Ta (°C)	-10	-10	0	0	-8	-8	0	0	
Max Wind Speed (m/s)	1	0.75	**-0.25**	**-25%**	1	0.75	**-0.25**	**-25%**	
Max Solar Rad (W/m^2)	200	200	0	0	200	200	0	0	
Min Humidity (%)	50	50	0	0	50	50	0	0	

Global Soil Microclimate Calculator simulations accurately reflect the effect of beech tree presence on percentage of shade, wind, and albedo in this study area, these results correspond to reasonable predictions of the micrometeorological impact of tree density in beech-dominated forests.

While macroclimate cooling can ameliorate hot and dry conditions, the impact of canopy cover on the subcanopy's micrometeorology has been shown to far outweigh the cooling effect on bare soil. Even with peak canopy openness, the influence of standing stock on microclimate remains observable. Thus, although microclimate researchers may need to incorporate other Earth systems like hydrology into their estimates of local environmental conditions, this simulation demonstrates the applicability of canopy and dominant vegetation data in contemporary DEB-based mechanistic niche models of forest-resident species. To validate the positive niche-construction ability of beech trees, as supported here by the observable amelioration of micrometeorology, further research would need to compare the ecophysiological benefit of a more amenable micrometeorology, as quantified here, with the cost of negative intraspecific effects. In beech trees, these negative effects may include competition for light, water, and nutrients as well as population density-dependent disease vectors. If establishment and recruitment outcomes remain higher for beech trees grown around conspecifics, then further population-level support would be found for net positive niche construction.

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Supplementary Material

Supplementary material referenced in the text of this article may be found online at https://doi.org/10.26443/msurj.v1i1.216.

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