# Modeled diversity effects on microbial ecosystem functions of primary production, nutrient uptake, and remineralization

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*Abstract.* Ecosystem-wide primary productivity generally increases with primary producer diversity, emphasizing the importance of diversity for ecosystem function. However, most studies that demonstrate this positive relationship have focused on terrestrial and aquatic benthic systems, with little attention to the diverse marine pelagic primary producers that play an important role in regulating global climate. Here we show how phytoplankton biodiversity enhances overall marine ecosystem primary productivity and other ecosystem functions using a self-organizing ecosystem model. Diversity manipulation numerical experiments reveal positive, asymptotically saturating relationships between ecosystem-wide phytoplankton diversity and functions of productivity, nutrient uptake, remineralization, and diversity metrics used to identify mechanisms shaping these relationships. Increase in productivity with increasing diversity improves modeled ecosystem stability and model robustness and leads to productivity rates that exceed expected yields primarily through niche complementarity and facilitative interactions between coexisting phytoplankton types; the composition of traits in assemblages determines the magnitude of complementarity and selection effects. While findings based on these aggregate measures of diversity effects parallel those from the majority of experimental outcomes of terrestrial and benthic biodiversity–ecosystem function studies, we combine analyses of community diversity effects and investigations of the underlying interactions among phytoplankton types to demonstrate how an increase in recycled production of non-diatoms through an increase in new production of diatoms drives this diversity–ecosystem function response. We demonstrate the important role that facilitation plays in the modeled marine plankton and how this facilitative interaction could amplify future climate-driven changes in ocean ecosystem productivity.

Key words: *California Current System; complementarity; diversity; ecosystem function; facilitation; marine ecosystem; niche; numerical model; nutrient uptake; phytoplankton; primary productivity; selection.*

## Introduction

In nature, productive ecosystems that efficiently use available resources generally show an increase in regionally averaged primary productivity with increasing diversity. Observations have shown this positive dependence for spatially structured benthic aquatic (Cardinale 2011) and terrestrial habitats, particularly in grasslands (Tilman et al. 2001). Similar positive relationships have also been observed in more spatially homogenous yet temporally dynamic pelagic environments (Ptacnik et al. 2010), primarily in closed, freshwater ecosystems (Behl et al. 2011), though one counterexample has been documented in freshwater phytoplankton bottle experiments with little natural diversity and environmental variability (Schmidtke et al. 2010). Marine phytoplankton communities exhibit tremendous diversity and play a regulatory role in the global climate (Falkowski 2012) and sensitivity to

environmental change (Behrenfeld et al. 2006, Boyce et al. 2010), yet observations characterizing pelagic diversity–ecosystem function relationships in open marine ecosystems are rare (Duffy and Stachowicz 2006).

In general, "ecosystem function" refers to any of a multitude of processes, including primary or secondary production, nutrient uptake, or remineralization, and three conceptual shapes are often used to characterize the typically positive functional relationship between diversity and ecosystem function (Cardinale et al. 2011; Fig. 1A–C). Considering primary productivity as an example, when productivity increases rapidly at low levels of producer diversity and saturates asymptotically at high levels a concave-down relationship results (Fig. 1A). Productivity can change approximately linearly with producer richness (Fig. 1B). Thirdly, rapid changes in productivity at high diversity produces a concave-up function (Fig. 1C), which is seldom observed (Cardinale et al. 2011) and could result in a catastrophic decline in productivity with small reductions in natural diversity levels. In the more commonly observed, concave-down relationship, robust ecosystem productivity remains
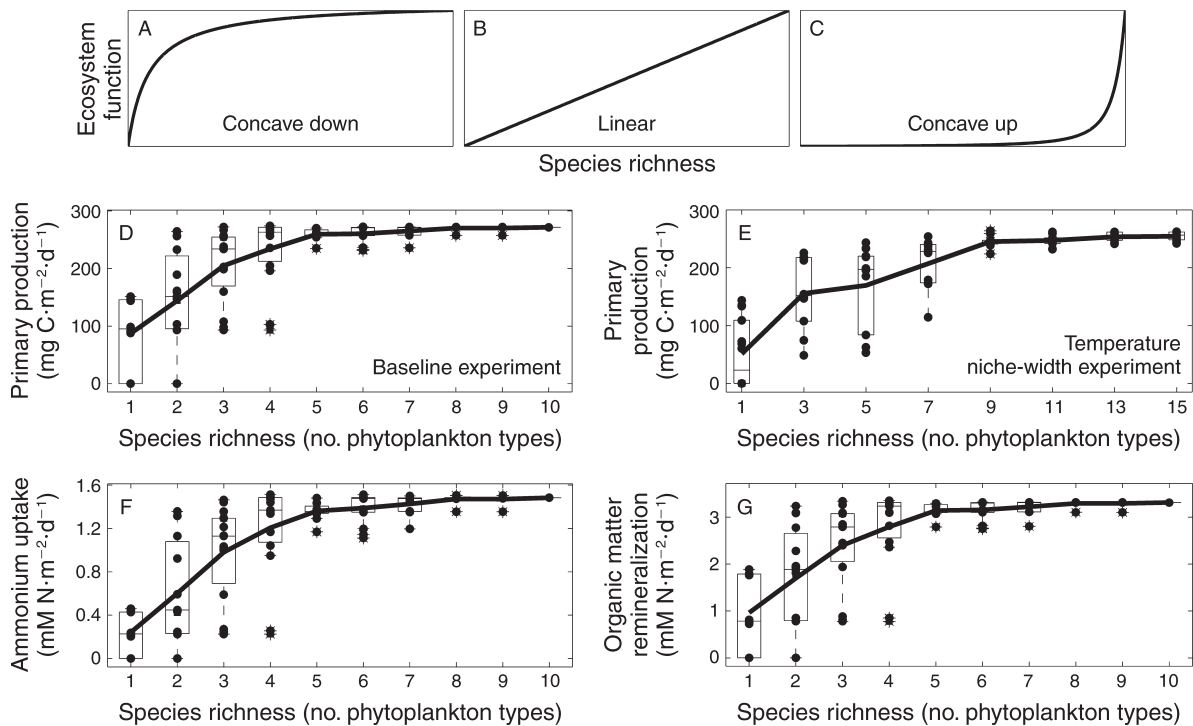
FIG. 1. Schematic representation of three positive relationships between ecosystem function and number of phytoplankton types: (A) concave down, (B) linear, and (C) concave up. The number of phytoplankton types for each ensemble is shown in relation to (D) regionally averaged productivity for baseline and (E) temperature niche-width experiments, and regionally averaged (F) ammonium uptake and (G) remineralization of particulate and dissolved organic matter for baseline experiments. Ensembles containing 1–5 phytoplankton types in the baseline experiment consisted of 15 replicates. The remaining ensembles in the baseline and temperature niche-width experiments consisted of 10 replicates. Ensemble means (heavy black lines) reveal a concave-down structure. Box plots show the median (thin black lines), 25th and 75th percentiles (box edges), the range in the most extreme data points excluding outliers (whiskers), and the outliers (points beyond ~2.7 SDs from the mean, shown as stars) for each ensemble. Similarly shaped relationships occurred for log-transformed response ratios and $D_{max}$, the deviation from maximum yield (see Appendix A: Fig. A1).

near natural diversity levels until extensive community degradation occurs; this scenario is sometimes described as the "rivet redundancy hypothesis" (RRH), drawing a parallel between the functional redundancy of species in an ecosystem and the rivets in an airplane that maintain function even as component loss occurs (Ehrlich and Ehrlich 1981, Cardinale et al. 2011).

Diversity effects of selection (or sampling) and complementarity provide aggregate measures of species interactions that can be used to interpret mechanisms linking diversity and ecosystem function. The *sampling effect* refers to the greater likelihood that high-yielding species are present in ecosystems with increasing species pool size (Huston 1997), and can set an upper bound on processes such as community productivity when this effect prevails (Tilman et al. 2001). The selection effect generalizes this concept, quantifying either positive or negative species performance in the community relative to that expected based on competition-free performance (Stachowicz et al. 2007). *Complementarity effects* include niche partitioning, facilitation, and negative interactions among coexisting species (Loreau et al. 2012), and reveal how a diverse community optimizes ecosystem func-

tioning through synergistic resource use (Stachowicz et al. 2007) beyond that attributed to a sampling effect (Tilman et al. 2001). Positive complementarity effects promote overyielding when a community outperforms that expected from results of constituent species in isolation. These diversity effects are not mutually exclusive (Hooper et al. 2005), and a comparison between the performance of species in monoculture and of an assemblage assess their relative importance. Such diversity-manipulation experiments in terrestrial grassland plots (Naeem et al. 1994, Tilman et al. 2001) and aquatic mesocosms (McGrady-Steed et al. 1997, Naeem and Li 1997, Cardinale 2011) demonstrate how these deterministic diversity effects point to mechanisms that drive changes in observed ecosystem processes. However, traditional experimental methods may also present confounding challenges, including temporal and spatial constraints, difficulties scaling up experimental results to ecosystem size, hazards choosing appropriate test species, rate-process measurement issues, and artificial sampling effects and hidden treatments (Huston 1997). In aquatic systems, parallel mesocosm experiments neglect advective dispersal mechanisms

(Finlay 2002) that may influence habitat connectivity and community composition.

Numerical ecosystem models offer an alternative, complementary approach to investigate the influence of diversity effects on ecosystem function in planktonic systems. While a recent analysis of a complex marine ecosystem model showed a similar, concave-down relationship between primary productivity and phytoplankton diversity (Prowe et al. 2012b), the experimental design did not allow for the calculation of diversity effects. In our present study we carry out numerical experiments that test the response of several ecosystem functions to diversity and are designed to quantify diversity effects on the functioning of the whole ecosystem. In addition, we investigate the underlying interactions to interpret these effects. This approach merges two distinct ecological perspectives, at the community and individual levels, to discern mechanistic underpinnings of the phytoplankton diversity–ecosystem function relationship. We hypothesize that diversity effects are responsible for maximizing total productivity in a marine ecosystem for a given physical circulation through niche differentiation and facilitation.

## METHODS

### Ecosystem model

A self-assembling, marine ecosystem model that represented phytoplankton diversity on a global scale (Follows et al. 2007, Barton et al. 2010) was coupled to a physical circulation model and evaluated for the California Current System (CCS; Goebel et al. 2010). The model domain, which has been used in several physical and biological studies (e.g., Broquet et al. 2009, Veneziani et al. 2009b, Drake et al. 2011, Moore et al. 2011), encompasses a broad portion of the CCS, extending along the U.S. west coast from mid-Baja, California, to the southern tip of Vancouver Island and offshore to 134° W (see Fig. 4 for domain extent). It is realistically forced at the ocean surface by output from the "coupled ocean–atmosphere mesoscale prediction system" (COAMPS; Hodur et al. 2002) and at lateral boundaries by the global ocean state estimate produced by ECCO (Estimating the Climate and Circulation of the Ocean; Wunsch et al. 2009). As documented in Veneziani et al. (2009a), the modeled California Current System undergoes a robust seasonal cycle in terms of sea surface temperature, sea surface height, and stratification. It exhibits pronounced wind-driven coastal upwelling during spring and summer and includes a vigorous ocean mesoscale field with reasonable eddy kinetic energy when compared to observations.

Embedded within this physical circulation is an ecosystem model representing multiple ecosystem functions. Primary production results from inorganic nutrient uptake by phytoplankton, which are grazed by zooplankton. Particulate and dissolved organic matter increase as a result of unassimilated grazing as well as phytoplankton and zooplankton mortality, and these

pools decrease through remineralization, which returns nutrients to ammonium, where nitrification converts this inorganic form to nitrite and then to nitrate (see Supplement for Fortran source code). Light for primary production is not spectrally resolved, but realistic shortwave radiation provided by COAMPS is converted to photosynthetically available radiation (PAR) using a constant value of 0.43. In the original version of the model, 78 stochastically parameterized phytoplankton types were divided into four functional groups. We applied a Holling type III grazing formulation that Prowe et al. (2012a) showed had an intermediate effect on diversity relative to contrasting grazing schemes that yielded higher or lower phytoplankton diversity but did not alter spatial patterns meaningfully. Realistic physical fields, including steep cross-shore gradients and strong seasonal and higher-frequency variability, drove interacting ecosystem components to produce biogeography and temporal variability of phytoplankton types commonly observed in the CCS (Goebel et al. 2010); large diatoms (DIA) peaked in coastal waters during the upwelling season and small phytoplankton types including cyanobacterial *Prochlorococcus*-like phytoplankton (PLP) and small non-*Prochlorococcus*-like phytoplankton (SNP) such as *Synechococcus* primarily peaked offshore during winter and early spring, respectively. Biological processes not included in the model, such as vertical migration and mixotrophy, limited representation of the fourth functional group that included large non-diatoms such as dinoflagellates (Goebel et al. 2010). We utilized this California Current System model to test the relationship between modeled phytoplankton diversity and ecosystem functions in a combinatorial numerical experiment.

### Experimental design

In a series of numerical experiments, we manipulated phytoplankton type richness to evaluate the effect of diversity on rate processes of primary productivity, nutrient uptake and availability, and remineralization of particulate and dissolved organic matter in the modeled CCS. Multi-year simulations of phytoplankton-rich communities reveal a distinct annual cycle in phytoplankton dynamics and community structure (Goebel et al. 2010). Simulations reported here extend over two model years (forced by realistic physical forcing and lateral boundary conditions for the years 1999 and 2000), with the first year discarded as a model adjustment period. We note that all runs exhibited seasonal variability in productivity and biomass except model experiments that included only PLP types; in our model, PLP are distinguished by their inability to use nitrate, and over time available ammonium and nitrite levels were converted to nitrate through nitrification, resulting in declining PLP populations. Community ecosystem processes were vertically integrated and averaged horizontally over the entire model domain and one year to encompass broad ecosystem response

over vast spatial area and a full annual cycle. In a one-year simulation with 78 phytoplankton types, average productivity for the 31 most productive types ranged over six orders of magnitude, and the 10 most productive types contributed over 99% of total averaged productivity. The model was re-run with random selections from these 10 major contributors. Fifteen replicates for polycultures containing two to five types, and 10 replicates for polycultures of six to nine types were constructed, plus an assemblage with the full complement of 10 types. Reducing the phytoplankton assemblage to its most productive components reduced but did not eliminate the likelihood of an artificial selection or sampling effect (Huston 1997). All simulations originated from one representative model realization and were initiated with the same environmental conditions to ensure measurement of a true diversity effect on the ecosystem rather than an effect of variable resource availability. Sensitivity of ecosystem productivity to different model realizations and pool size of randomly selected phytoplankton types demonstrated model robustness (Appendix D).

Availability of ecological niches impacts ecosystem diversity. To test for a niche effect on the number of phytoplankton types necessary to maximize modeled ecosystem productivity, we performed an additional set of experiments in which each phytoplankton type's unique temperature niche width was reduced by one half by altering the decay constant of the temperature response formulation (Goebel et al. 2010). Of 78 modeled phytoplankton types, the most productive 26 types contributed 99.9% to total assemblage productivity. Similar to the baseline experiment described above, these 26 phytoplankton types characterized by narrow temperature niche widths were tested in the model as monocultures and ensembles of polycultures consisting of 3 to 15 randomly drawn types. Each ensemble contained 10 unique model assemblages.

### Diversity-effect calculations

Various metrics were utilized to assess the effects of diversity on modeled ecosystem function, including measures of relative yield, net effect, complementarity effect, selection effect, $D_{max}$ (deviation from maximum yield; Loreau 1998), and log-transformed response ratios. Modeled relative yield, measured as the ratio of the performance of a phytoplankton type in the assemblage to that in monoculture (Hector 1998, Loreau 1998), was used to assess the performance of each phytoplankton type. A high relative yield indicated high performance regardless of competition. To evaluate the aggregate effect of different functional types on ecosystem function, a net effect (NE) was quantified as the difference in performance between modeled assemblage function and that expected from the constitutive monocultures (Loreau and Hector 2001). Decomposition of the NE into additive complementarity and selection effects (CE and SE, respectively) was used to

quantify aggregate responses and interactions between phytoplankton types (Loreau and Hector 2001). A positive CE, on average, occurs if polyculture performance relative to that in monoculture exceeded that from initial seeding and does not reflect competition between types. A positive SE occurs when one or more highly performing phytoplankton types in monoculture also dominate the polyculture by outcompeting other types. A negative SE indicates high polyculture performance of low-performing monoculture types.

Fox (2005) argues that the SE may not exclusively reflect dominance by a type characterized by specific traits and at the expense of others, according to the original intent of this calculation based on natural selection. He demonstrates that the SE may also encompass the success of a species characterized by specific traits without compromising others. As a result, Fox (2005) further partitions the SE of Loreau and Hector (2001) into effects associated with and without competition, referred to as a dominance effect (DE) and a trait-dependent complementarity effect (TDCE), respectively, and refers to the CE of Loreau and Hector (2001) as the trait-independent complementarity effect (TICE). Both TDCE and TICE do not occur at the expense of other types (e.g., through competition), and these metrics reveal the improved performance of types with certain traits (TDCE) or all types in the assemblage (TICE) relative to monoculture performances. DE, TDCE, and TICE comprise the newly derived "tripartite partition" and provide interpretations for the mechanisms linking diversity and ecosystem function (Fox 2005), as expanded upon in the Appendix A. For a simplified example, we also apply these calculations and interpretations of diversity effects to two-member ensembles (Appendix B and Table B1).

$D_{max}$ and log-response ratios (Hedges et al. 1999) for the maximum and net effects ($LR_{max}$ and $LR_{net}$) offer general, widely applicable metrics to measure diversity effects by comparing extremes which allow for cross-comparison among studies (Appendix A).

### RESULTS

Output from the numerical experiments revealed asymptotically saturating, concave-down relationships between diversity and productivity for the entire domain (Fig. 1D) and subregions (Appendix C and Fig. C1). Based on the ensemble average, a random selection of five phytoplankton types were required to nearly maximize ecosystem function. Ensembles that contained five or more types were, on average, 75% more productive than the mean of the ensembles containing two types, but less productive than the most productive two-member polycultures. Some two-phytoplankton type polycultures attained levels of productivity within a few percentage points of the 10-member assemblage, suggesting a sampling effect (Appendix B and Table B1). Asymptotic trends also characterize the relationship between diversity and rates of $NH_4$ uptake, remineral-
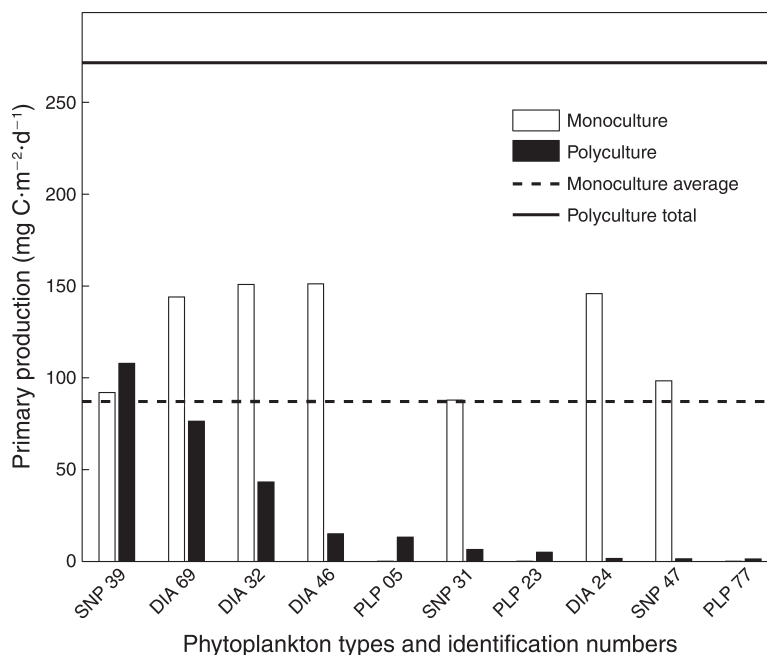
Fig. 2.    Differences in spatially and temporally averaged, vertically integrated primary productivity of each phytoplankton type in monoculture and 10-member polyculture. The x-axis order of phytoplankton types (left to right) is ranked in order of decreasing contribution to polyculture productivity. Horizontal lines show average monoculture and total polyculture productivity. The phytoplankton codes are: DIA, diatom; PLP, cyanobacteria *Prochlorococcus*-like phytoplankton; and SNP, small non-PLP phytoplankton.

ization of particulate and dissolved organic matter (Fig. 1F, G), diversity metrics (Appendix A: Fig. A1), and ammonium concentration (not shown). An alternate presentation of these results, defining species richness as the number of functional groups rather than phytoplankton types, also shows increased ecosystem function with species richness. In Fig. E1 of Appendix E average productivity increased monotonically with numbers of functional groups, although the most productive two-functional-group experiment was as productive as the most productive experiment with three functional groups.

The number of phytoplankton types required to maximize ecosystem function and the slope of the richness–ecosystem function relationship can be modified by adjusting the niche width of phytoplankton types (Fig. 1E). Decreasing the temperature niche width of all modeled phytoplankton types by one half reduced the slope of the diversity–productivity relationship and approximately doubled (9 types) the number of phytoplankton types necessary to saturate the ensemble average system productivity when compared to baseline simulations (Fig. 1E). Decreasing the niche width of phytoplankton types increased the number of ecological niches available and therefore allowed for greater diversity. Increased niche availability resulted in a more gradual loss in productivity as richness declined.

Comparison of the performance of each phytoplankton type in the 10-member assemblage to their performance in monoculture (Fig. 2) demonstrated that

phytoplankton types were not always more productive in monoculture than in the assemblage, as for all diatoms (DIA) and the two least productive small non-*Prochlorococcus*-like phytoplankton (SNPs 31 and 47). The most productive SNP and all three PLPs (*Prochlorococcus*-like phytoplankton) were more productive within the assemblage than in monoculture. The high relative yields of these four phytoplankton types drove the polyculture productivity to exceed the mean and highest monoculture productivity (Fig. 2).

The *net diversity effect* (NE), defined as the difference between productivity of the assemblage and that expected from the constitutive monocultures, was positive and substantial (185 mg $C \cdot m^{-2} \cdot d^{-1}$) for the 10-member polyculture, decreasing asymptotically with decrease in ensemble size and producing more than a factor of 3 times the productivity of the monoculture average (Fig. 3). The 10-member polyculture also exceeded the maximum monoculture productivity. Diversity metrics of log-response ratios and $D_{max}$ (deviation from maximum yield; Loreau 1998) were positive and increased asymptotically with increase in richness also saturating for five-member assemblages (see Appendix A: Fig. A1). In the 10-member assemblage, six of the member's yield (SNP 39, DIA 69, DIA 32, PLP 5, PLP 23, and PLP 77) showed greater fitness and exceeded their expected yield based on monoculture values (Appendix A: Table A1.A). Large positive complementarity ($4.8 \times 10^{-5}$ mg $C \cdot m^{-2} \cdot d^{-1}$) and negative selection effects ($-4.8 \times 10^{-5}$ mg $C \cdot m^{-2} \cdot d^{-1}$)
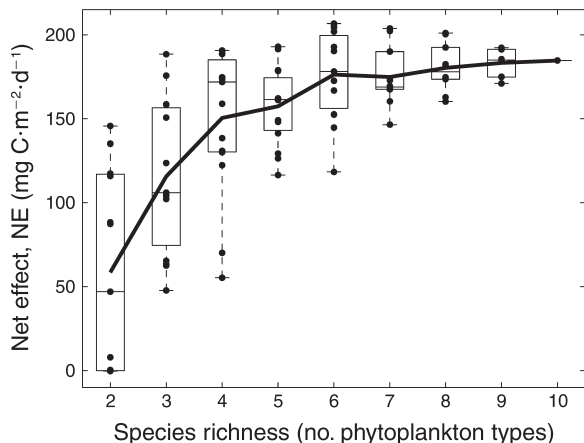
F_IG. 3.  Net diversity effect vs. the number of phytoplankton types in the assemblage shows that, on average, an increase in assemblage size not only increases ecosystem productivity (see Fig. 1), but also increases the amount that assemblage productivity exceeds that expected from constituent monocultures. Ensembles containing 1–5 phytoplankton types consisted of 15 replicates. The remaining ensembles consisted of 10 replicates. Lines, symbols, and box plots are as described for Fig. 1.

resulted from diversity-effect calculations (Appendix A: Table A1.B). Further partitioning the selection effect of Loreau and Hector (2001) into the dominance and trait-dependent complementarity effects of Fox (2005) resulted in a small negative dominance effect (–0.87 mg C·m$^{-2}$·d$^{-1}$) and substantial negative trait-dependent complementarity effect (–4.8 × 10$^{-5}$ mg C·m$^{-2}$·d$^{-1}$) (Appendix A: Table A1.B). The very large magnitudes of the selection and complementarity (or trait-dependent complementarity) effects resulted from the exceedingly low productivity of PLP in monoculture. As described above, PLPs were not well suited to monoculture experiments because nitrification reduces available ammonium and nitrite, which PLP require, in favor of nitrate. As a result, PLP monocultures show declining biomass and productivity over time. Calculations from 1999 and 2001 reveal considerably smaller and larger absolute values of selection and complementarity, respectively, although the net diversity effect and overall conclusions are not altered meaningfully (not shown).

Variance in ensemble member productivity (and other ecosystem processes) decreased with an increase in producer richness (Fig. 1D–G) and the number of functional groups (Appendix E: Fig. E1), indicating a favorable impact of higher diversity. Productivity variance for the two-member polyculture ensemble was an order of magnitude greater than that for ensembles of polycultures containing five or more types. Similarly, variance of the ensemble with two functional groups was an order of magnitude greater than that having three functional groups.

While five randomly selected phytoplankton types were on average needed to approximately maximize

productivity and most efficiently utilize available resources under the baseline parameterized model formulation tested here, the types that made up this community varied (Fig. 4 and Table 1). For example, a comparison of runs 3, 11, and 15 show that different combinations of phytoplankton types consisting of three DIA (from type numbers 24, 32, 46, 69), 1 to 2 SNP (from 39, 47), and 0 to 1 PLP (77) attained an identical average productivity rate (269 mg C·m$^{-2}$·d$^{-1}$; Fig. 4 and Table 1). While more than one trait combination could attain a similar productivity rate, the percentage contribution of these phytoplankton types varied and was dominated (range, 62%–89%; mean, 73.6%) by two types consisting of 1 DIA and 1 SNP in 14 out of 15 model runs (Table 1). Regardless, all members of the community made detectable contributions of at least 1.9% to the total, except for two instances in which a DIA 24 contributed 0.6% (Table 1).

DISCUSSION

In agreement with global model results (Prowe et al. 2012b), output from this regional model revealed an asymptotically saturating, concave-down relationship between phytoplankton diversity and productivity that conformed to the predominant rivet redundancy hypothesis (RRH; Ehrlich and Ehrlich 1981, Cardinale et al. 2011) pattern observed across many terrestrial and aquatic studies (Fig. 1D, E). The emergence of this relationship for other modeled ecosystem processes (nutrient uptake and decomposition; Fig. 1F, G) and diversity metrics (NE [net effect], log-transformed response ratios, and $D_{max}$ (deviation from maximum yield; Loreau 1998); Fig. 3; Appendix A: Fig. A1) demonstrates the robust link between modeled phytoplankton diversity and ecosystem function. These relationships and diversity-effect metrics provide insight into the mechanistic underpinnings that shape these positive relationships.

Calculations for the NE, $D_{max}$, and log-transformed response ratios all indicate transgressive overyielding of assemblages containing five or more phytoplankton types for the baseline experiment. A large, positive complementarity effect (CE) indicates that overyielding of the assemblage is attributed to niche complementarity and possibly facilitation. The partitioning of the NE into SE (selection effect) and CE (Loreau and Hector 2001) results in an accompanying, large negative SE. Negative SE values result when species with low monoculture yields outperform their expected relative yields in assemblage, as is true here for Prochlorococcus-like phytoplankton (PLP) types. To better identify dominance of advantaged species, such as the most productive small non-PLP (SNP) and diatoms (DIAs) (Fig. 2), we further partitioned the SE of Loreau and Hector (2001) into dominance effects (DE) and trait-dependent complementarity effects (TDCE) after Fox (2005). The resulting very small magnitude DE and large value for TDCE indicate that success of smaller phytoplankton
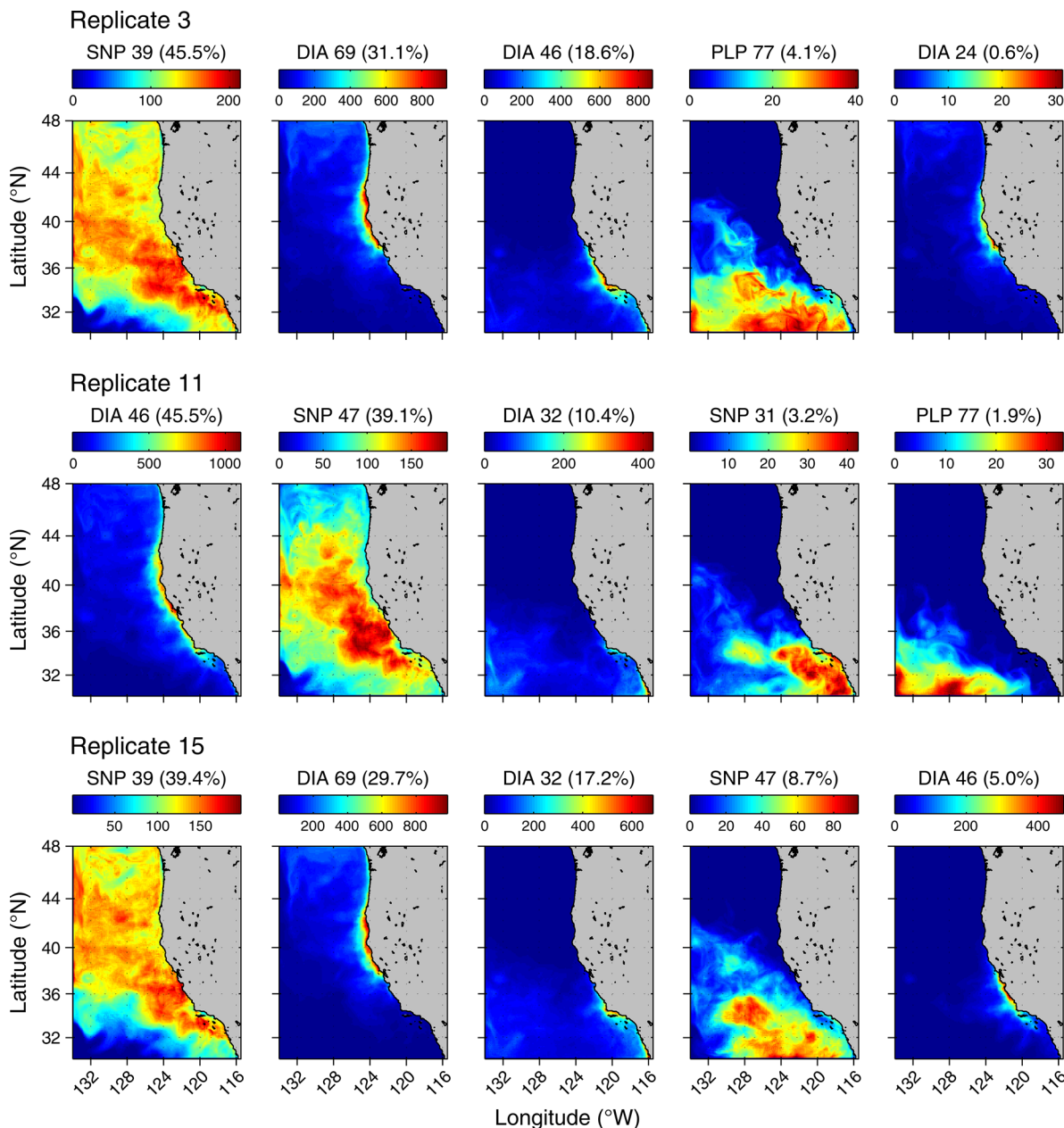
FIG. 4. Annually averaged (year 2000), vertically integrated primary productivity (individual color key bars; mg C·m$^{-2}$·d$^{-1}$) in the California Current System (U.S. West Coast from mid-Baja to the southern tip of Vancouver Island and offshore to 134° W) for three different assemblages (replicates 3, 11, and 15) each containing five phytoplankton types. Phytoplankton type (and percentage contribution) are shown above each plot. See Fig. 2 legend for phytoplankton type codes; see Table 1 for the percentage contributions of other five-type assemblages not shown here.

types does not arise through direct competition with (i.e., at the expense of) highly productive types, but rather in addition to their success.

Together, these values suggest a facilitation effect resulting from phytoplankton types coexisting in the California Current System (CCS; Goebel et al. 2010), with assemblage production enhancing the specialized niche to which PLP are well adapted. In our model,

increased diversity increases the efficiency of production within various ecosystem niches. The associated increase in biomass with increase in productivity stimulates grazing and remineralization of organic matter, and thus increased ammonium availability and its uptake (see Fig. 1D, F, G). This cycle is well known in oceanography, but usually expressed in terms of new and recycled production (Dugdale and Goering 1967);

TABLE 1.  Percentage contribution of each phytoplankton type to assemblage average primary productivity (PP) for 15 different modeled assemblages containing five members.

| Model run no. | Phytoplankton type and identification number | | | | | | | | | | PP (mg C·m⁻²·d⁻¹) |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | SNP 39 | DIA 69 | DIA 32 | DIA 46 | PLP 05 | PLP 31 | PLP 23 | DIA 24 | SNP 47 | PLP 77 | |
| 4 | 42.2 | 31.2 | — | 17.2 | 6.8 | — | 2.6 | — | — | — | 270 |
| 12 | 44.2 | — | 20.4 | 5.9 | — | — | — | 25.5 | — | 4.0 | 269 |
| 3 | 45.5 | 31.1 | — | 18.6 | — | — | — | 0.6 | — | 4.1 | 269 |
| 15 | 39.4 | 29.7 | 17.2 | 5.0 | — | — | — | — | 8.7 | — | 269 |
| 7 | 46.4 | 27.9 | 19.4 | 5.7 | — | — | — | 0.6 | — | — | 263 |
| 11 | — | — | 10.4 | 45.5 | — | 3.2 | — | — | 39.1 | 1.9 | 259 |
| 2 | — | — | — | 20.4 | 6.1 | 4.9 | — | 28.1 | 40.5 | — | 259 |
| 13 | — | — | 23.7 | — | 5.1 | — | 2.3 | 30.4 | 38.5 | — | 258 |
| 1 | — | — | — | — | 3.7 | 5.2 | 3.1 | 46.2 | 41.8 | — | 258 |
| 8 | — | 30.4 | 23.0 | — | — | 2.9 | 5.6 | — | 38.2 | — | 258 |
| 9 | — | — | 15.7 | 10.6 | — | — | — | 27.3 | 43.1 | 3.3 | 257 |
| 10 | — | 21.0 | 23.1 | — | — | — | 7.0 | 9.6 | 39.4 | — | 257 |
| 5 | — | 31.7 | — | — | 5.2 | — | 3.2 | 15.3 | 44.6 | — | 256 |
| 14 | — | 19.7 | 14.9 | 10.9 | — | — | — | 8.1 | 46.4 | — | 255 |
| 6 | — | 17.2 | — | 25.0 | — | 35.7 | 7.9 | 14.1 | — | — | 235 |

*Notes:* Model run number is listed from most to least productive. A dash in a cell indicates that those phytoplankton types were not used in that model run.

new production is broken down by microbial processes to ammonium and, through nitrification, nitrite and nitrate, stimulating recycled production. In our model, enhanced diversity increased nutrient recycling that facilitated PLP growth due to its competitive superiority for ammonium and nitrite. This advantage allowed them to compete with other phytoplankton types, particularly in regions of low nitrate such as offshore zones that are far removed from the new nitrogen from coastal upwelling. Further increases in system-wide productivity resulted from additional recycling of PLP production. Thus our model demonstrates how facilitation, in addition to the complementarity effect of niche partitioning, contributes to a positive net diversity effect in a planktonic marine ecosystem.

In two-member polyculture experiments that did not include PLP but did have SNP and a diatom, the facilitation effect contributed to increased concentrations of SNP, which (having faster ammonium-based uptake rates than diatoms but slower than PLP) fulfilled the analogous role in more limited communities (Appendix B and Table B1). Monocultures and polycultures that included PLP exclusively resulted in declining biomass over time, further emphasizing the facilitative role that recycling plays in this ecosystem.

Variability among replicated simulations at each richness level indicated an increase in ecosystem stability with increasing richness, both in terms of phytoplankton types (Fig. 1) and functional groups (Appendix E: Fig. E1). Although several possible metrics for ecosystem stability exist (e.g., related to multiple equilibria, invisibility, and extinction) here we focus on variance reduction (Ives and Carpenter 2007). Decreasing variance with increasing diversity may be explained by the variance-reduction effect, defined as the increased probability in the degree of similarity of replicate mixed assemblages with increase in phytoplankton richness

(Huston 1997). Increased ecosystem stability is also promoted by overyielding when, for example, an increase in ecosystem function with diversity exceeds its standard deviation (Cardinale et al. 2012), as occurs here. Reduced variability in ecosystem functions at high levels of richness concurs with the idea that functional redundancy of species that respond differently to environmental conditions leads to a more stable ecosystem (McGrady-Steed et al. 1997, Naeem and Li 1997, Ives and Carpenter 2007) and predictable model.

Lastly, variation in the trait composition of phytoplankton assemblages, despite equivalent total productivity among replicates equivalent in richness, revealed a composition effect. This outcome reflects protist communities in nature that are dominated by few, but include many rare taxa (Caron and Countway 2009), as well as observations in experiments manipulating terrestrial diversity in which rarer species made small but detectable contributions despite dominance by 5–10 species that explained the majority of the diversity effects (Tilman et al. 2001). As declared by Hooper et al. (2005), even rare species may strongly impact ecosystem function. Further, the functional redundancy of this elusive or "rare biosphere" is not only ecologically important in a changing environment (Caron and Countway 2009), but also has potential to increase in importance over time (Cardinale et al. 2007, Reich et al. 2012). The effect of community composition on productivity highlights that functional-trait composition is at least as important as richness for the functioning of the modeled phytoplankton community.

## Conclusion

Positive primary productivity–diversity relationships that emerge for terrestrial, freshwater, and marine ecosystem types underscore potentially adverse functional consequences of species loss. However, it has been

argued that microbial diversity is integral to ecosystem function and may never diminish to a level that impairs ecosystem function (Finlay et al. 1997). In our study, the diversity level at which an ecosystem function begins its decline is low, it depends on ecological niche width, and fewer niches create a more precarious drop in ecosystem productivity as richness declines. Quantitative identification of phytoplankton niches in nature is challenging, but novel approaches such as determining the probability that specific species are observed given certain environmental conditions (Irwin et al. 2012) are characterizing realized niche width. Their identification in the North Atlantic of a large number of overlapping niches for diatoms and dinoflagellates suggests that the present ocean is far from low diversity levels.

Rather, the primary impact of phytoplankton diversity on ecosystem function in a changing environment may be indirect. In one scenario of warming ocean surface, vertical nutrient flux accompanying a deeper thermocline and increased stratification is predicted to decline (Di Lorenzo et al. 2005). Increased surface temperatures and stratification are suspected drivers of global declines in phytoplankton biomass (Boyce et al. 2010) and productivity (Behrenfeld et al. 2006), and shifts from diatom to toxic dinoflagellate dominance in California's coastal ocean (Jester et al. 2009; R. M. Kudela, M. Kahru, J. P. Ryan, and D. G. Foley, *unpublished manuscript*). Lower nutrient flux is likely to reduce new productivity of large, rapidly growing phytoplankton types such as diatoms (Chavez et al. 1991, Goebel et al. 2013), and a reduction in new production will result in larger declines in ecosystem-wide, total productivity by, as our study shows, removing overyielding effects of recycled production. In contrast, alternative climate predictions of increased nutrient flux to California coastal waters resulting from basin-scale changes in nutrient supply to upwelled source waters (Rykaczewski and Dunne 2010) or increased vertical transport associated with stronger equatorward wind stress (Bakun 1990, Auad et al. 2006) could promote a positive feedback between increased diatom and non-diatom growth that boosts ecosystem-wide productivity beyond current levels. These results suggest resilient marine ecosystems in which diversity amplifies directly driven changes to ecosystem function in the ocean.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Additional diversity-effect interpretations and calculations (*Ecological Archives* E095-014-A1).

### Appendix B

Simplified application and interpretation of diversity effects for two-member-ensemble calculations (*Ecological Archives* E095-014-A2).

### Appendix C

Diversity–productivity relationship in coastal and offshore domain-subregions calculations (*Ecological Archives* E095-014-A3).

### Appendix D

Variation among model realizations and random selection of phytoplankton-types calculations (*Ecological Archives* E095-014-A4).

**Appendix E**

Functional-group–productivity relationship calculations (*Ecological Archives* E095-014-A5).

**Supplement**

Fortran source code for the self-assembling ecosystem model that is coupled to the Regional Oceanographic Modeling System (ROMS) calculations (*Ecological Archives* E095-014-S1).