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LETTERS

Diversity and dispersal interactively affect predictability of ecosystem function

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Theory and small-scale experiments predict that biodiversity losses can decrease the magnitude and stability of ecosystem services such as production and nutrient cycling[1,2]. Most of this research, however, has been isolated from the immigration and emigration (dispersal) processes that create and maintain diversity in nature[3–5]. As common anthropogenic drivers of biodiversity change—such as habitat fragmentation, species introductions and climate change—are mediated by these understudied processes[5–7], it is unclear how environmental degradation will affect ecosystem services[3,4]. Here we tested the interactive effects of mobile grazer diversity and dispersal on the magnitude and stability of ecosystem properties in experimental seagrass communities that were either isolated or connected by dispersal corridors. We show that, contrary to theoretical predictions[2,8–11], increasing the number of mobile grazer species in these metacommunities increased the spatial and temporal variability of primary and secondary production. Moreover, allowing grazers to move among and select patches reduced diversity effects on production. Finally, effects of diversity on stability differed qualitatively between patch and metacommunity scales. Our results indicate that declining biodiversity and habitat fragmentation synergistically influence the predictability of ecosystem functioning.

Broadening the spatial scope of biodiversity–ecosystem-functioning (BD–EF) research to metacommunities—that is, groups of patches connected by dispersal of organisms—adds two components of diversity: beta-diversity, or heterogeneity in species composition among patches, and gamma-diversity, or diversity of the entire metacommunity[12]. Limited evidence indicates that, at these broader spatial scales, the functional consequences of diversity may be different[13,14]. Furthermore, the effects of dispersal among patches on ecosystem properties have rarely been considered, despite the demonstrated importance of dispersal in maintaining diversity, particularly in fragmented habitats[5,10,15]. Given recent predictions that the mechanism of diversity maintenance strongly influences relationships between biodiversity and ecosystem function[15,16], and the increasingly fragmented character of most habitats, scaling up BD–EF research to metacommunities is critical for its application to conservation.

Here we test how diversity, dispersal and spatial scale interactively affect properties of experimental multitrophic seagrass (*Zostera marina*) ecosystems. We assembled metacommunities with low (three spp.) and high (eight spp.) grazer species richness, simulating loss of rare species from a species pool. Each metacommunity had five patches that were either interconnected by dispersal corridors or unconnected (see Methods). Dispersal was extremely rare among unconnected patches and moderate among connected patches. Each patch received 30 mobile crustacean grazers (15 male–female species pairs), and the species composition of this founding community was determined by random draws from the appropriate species list (three versus eight spp.). Initial metacommunity-wide richness of grazers was set at either three or eight species, but both the relative abundances of species within metacommunities and the species richness within patches varied. We allowed this initial random assembly plus subsequent dispersal and species interactions to influence grazer diversity over the six-week-long experiment. This enabled us to determine how multiple spatial components of biodiversity affect ecosystem properties in both connected and unconnected metacommunities.

We tested four hypotheses. (1) Increasing metacommunity richness will increase mean patch richness[15,17] and beta-diversity of grazers[18]. (2) Allowing dispersal will increase mean patch richness[5,15] and decrease beta-diversity[17] of grazers. On the basis of these predicted diversity patterns, and on previously documented links between diversity and ecosystem properties[1], we expected that (3) grazer abundance and grazing pressure will increase with metacommunity richness and dispersal[13,15–17]. As increasing richness often increases the predictability of ecosystem properties[2,8–11], even in multitrophic systems[19] and in metacommunities[15], we also hypothesized that (4) increasing metacommunity richness should increase predictability of ecosystem properties among and within patches.

Both metacommunity richness and dispersal of grazers influenced grazer diversity (Fig. 1a–c). As predicted, increasing initial metacommunity richness increased final grazer diversity at all scales: within patches (alpha-diversity), between patches (beta-diversity), and within entire metacommunities (gamma-diversity)[15,17]. Grazer dispersal increased compositional similarity among patches, decreasing beta- and gamma-diversity without affecting alpha-diversity in the patches (Fig. 1a–c). Both local extinctions and colonizations occurred, at varying rates for different species (Supplementary Table S1). Dispersal was frequent enough that all but one grazer species successfully founded populations in patches where they were not initially present, colonizing 25–100% of such patches. But dispersal was not so frequent that it erased the stamp of initial composition, as the final proportional abundances of most species were significantly predicted by initial proportional abundances (Supplementary Table S1). This evidence of colonization, extinction and moderate dispersal rates confirms that our connected patches functioned as true metacommunities. The effects of this active dispersal on diversity in our experiment parallel the effects of passive dispersal observed for protozoans and other zooplankton[20,21], indicating that the dispersal effects on metacommunity diversity we found may be robust.

Metacommunity richness and dispersal of grazers also affected net production at multiple trophic levels. Mean grazer abundance increased with grazer richness, both within patches (Supplementary Table S2) and in entire metacommunities (Fig. 2a), as predicted[13,15–17]. Concomitantly, the larger populations of grazers in richer metacommunities more effectively cropped biomass of primary producers,

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including macroalgae, cyanobacteria, the foundation species (*Zostera*), and its epiphytic algae (Fig. 2c–f; Supplementary Table S2). These metacommunity-richness effects cannot be explained by 'selection effects' (that is, presence of a particular species at higher diversity), because several species from both small and large pools significantly contributed to these trends (see Supplementary Methods). Thus, even in a system with random assembly, immigration and emigration, species richness pervasively influenced community and ecosystem properties.

Compared with diversity, grazer dispersal had relatively modest effects on ecosystem properties. Contrary to our prediction[5,15], dispersal did not increase mean grazer diversity or abundance within patches (Fig. 1a–c, Fig. 2b). Nonetheless, dispersal did affect grazing impact, allowing grazers to actively seek patches with preferred food and abandon patches with undesirable food. Specifically, connecting patches decreased the biomass of edible macroalgae and recruits of the tunicate *Molgula manhattensis* (Fig. 2c, d). In contrast, dispersal increased the biomass of less preferred cyanobacteria and *Z. marina*, at least in the less diverse communities (Fig. 2e, f). During the first 28 days of the experiment, this dispersal-mediated shift in grazing impact actually enhanced epiphyte biomass accumulation within connected patches (Supplementary Table S2). Furthermore, connecting patches reduced the enhancement of secondary production by diversity seen in isolated patches. Specifically, total grazer abundance increased with grazer diversity, but the slope of this relationship was reduced by grazer dispersal (Fig. 2b; Supplementary Table S3). In the absence of dispersal, diversity led to more effective and thorough grazing; however, when grazers could actively select favourable patches, they may have limited their own population growth by indirectly facilitating the colonization of limited substrate by less palatable algae[22]. Hence, active dispersal and habitat selection by multiple generations of grazers can affect ecosystem properties and modify the effects of biodiversity on ecosystem properties, underscoring a key difference between assemblages with single versus multiple trophic levels.

Also contrary to our expectations[2,8–11], higher metacommunity richness increased ecosystem variability both among and within patches. Although the similarity hypothesis predicts that increasing diversity increases compositional similarity, thereby increasing the predictability of ecosystem function across space[11], we found that more diverse grazer metacommunities produced greater spatial variability in ecosystem properties, including algal and sessile invertebrate biomass accumulation (Fig. 3b–d). This increased spatial variability probably stemmed from variability in grazer community composition (increased beta-diversity) in the more diverse metacommunities (Fig. 1b), supporting the hypothesis that compositional similarity and spatial predictability of ecosystem function are positively related[11]. However, these results also indicate that when

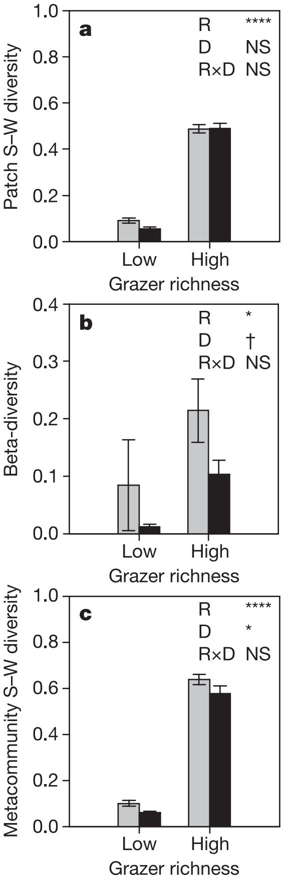

Figure 1 | Species pool size affects grazer diversity at multiple spatial scales. Grey bars indicate no dispersal corridors; black bars indicate dispersal corridors. **a**, Mean (±s.e.m.) patch diversity (Shannon–Weaver (S–W); $n = 25$ for each bar). **b**, Beta-diversity (see Supplementary Methods (Diversity Measures); $n = 5$ for each bar). **c**, Metacommunity S–W diversity ($n = 5$ for each bar). R, richness; D, dispersal; †, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$; NS, not significant.

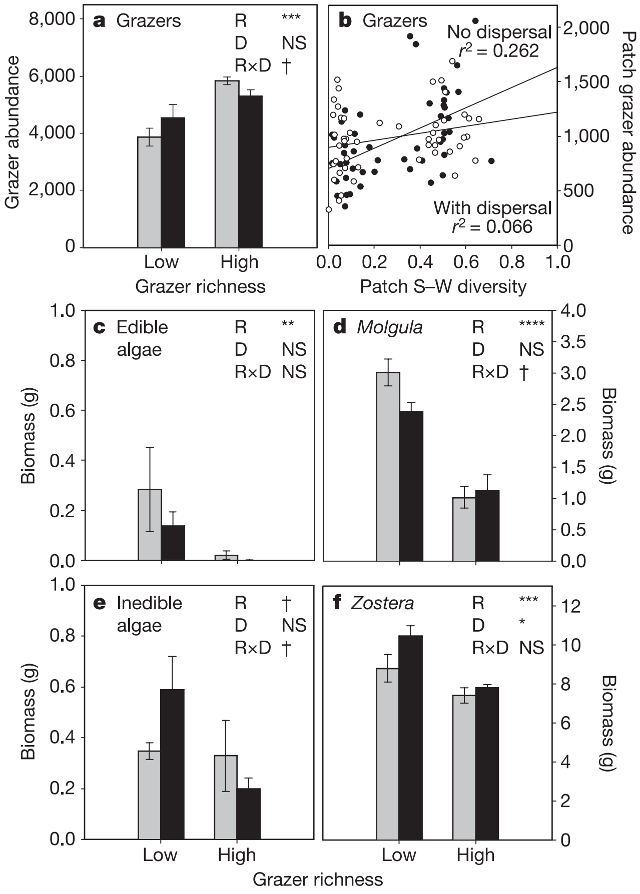

Figure 2 | Metacommunity richness and dispersal affect the magnitude of ecosystem properties at multiple trophic levels. a, **b**, Mean (±s.e.m.) grazer abundance increased with diversity (**a**), but this relationship was modified by dispersal (**b**). In **b**, open symbols indicate no dispersal; closed symbols indicate dispersal. For each set, $n = 50$. **c**–**f**, More diverse (and denser) grazer communities more effectively reduced biomass of edible macroalgae (**c**), *M. manhattensis* recruits (**d**), less edible cyanobacteria (**e**), and *Z. marina* (the foundation species) (**f**). Connecting patches allowed grazers to concentrate on preferred food (**c**, **d**), facilitating accumulation of less preferred food (**e**, **f**). For each bar, $n = 5$. Symbols are as in Fig. 1.

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species are lost from entire landscapes—and not just local communities—declining diversity may increase patch compositional similarity, producing a negative relationship between diversity and predictability in space. The contrast between our results and previous experiments[11,23,24] highlights the importance of examining how different biodiversity-loss scenarios affect ecosystem function, and recognizing that higher diversity does not necessarily increase the predictability of ecosystem functioning in space as it often does in time.

Metacommunity grazer richness also affected temporal variability of ecosystem properties, but in surprising, scale- and dispersal-dependent ways. Temporal variabilities of both grazer abundance and epiphyte load were generally lower in metacommunities than in patches (Fig. 3e–h). At the patch scale, increasing grazer richness increased temporal variability of grazer abundance (Fig. 3e), contradicting predictions that diverse competitive assemblages will have lower temporal variability of aggregate properties[2,8–10,15]. Our results are consistent, however, with recent theory predicting that biodiversity can reduce stability of biomass in multitrophic food webs with strongly generalist grazers, like ours[19], and that mobile consumers can destabilize production in patchy landscapes[25].

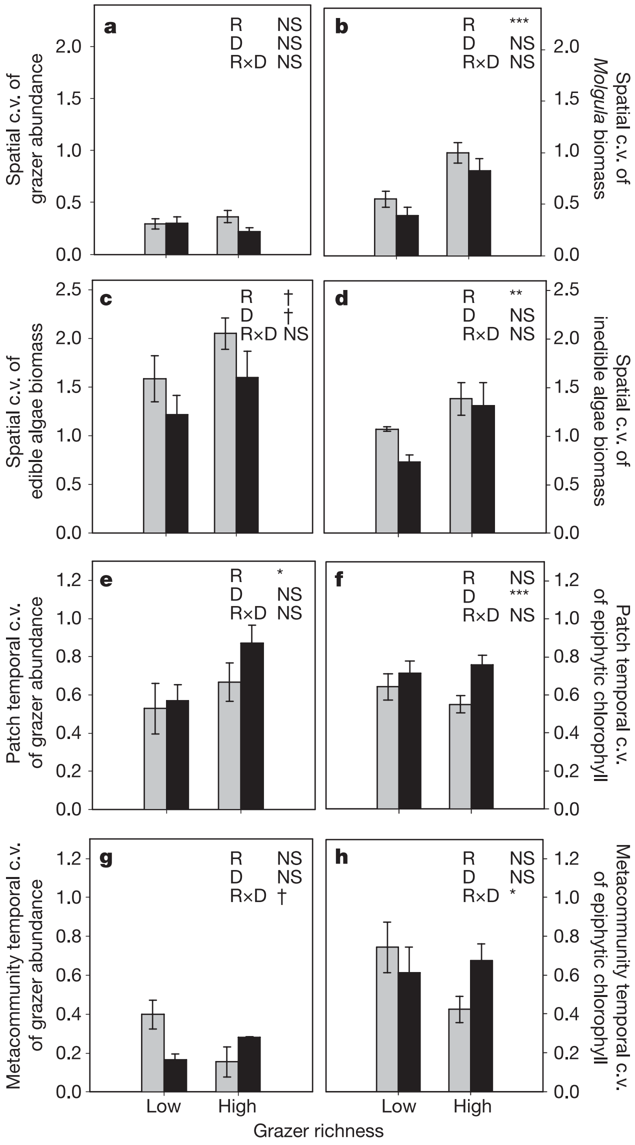

Figure 3 | Diversity effects on ecosystem variability are modified by dispersal and spatial scale. a–d, Spatial variation (c.v.) (±s.e.m.) among the five patches within a metacommunity for grazer abundance (**a**), biomass of *Molgula* (the most frequent sessile invertebrate invader) (**b**), edible algae biomass (macroalgae) (**c**), and inedible algae biomass (cyanobacteria) (**d**). For each bar, $n = 5$. **e–h**, Temporal variation (c.v.) (±s.e.m.) of grazer abundance (**e**, **g**) ($n = 10$) and epiphyte load (**f**, **h**) ($n = 25$) within patches and within whole metacommunities. Symbols are as in Fig. 1.

In contrast to patch-scale patterns, at the metacommunity scale diversity stabilized both grazer and epiphyte abundance, at least in the absence of dispersal (Fig. 3g, h), confirming predictions[2,8–10,15]. As the patches in these unconnected metacommunities were isolated, the reduced variability of their summed properties at high diversity—even while individual patch variability was increased—must be due to asynchronous fluctuations. Asynchrony is often invoked as a mechanism stabilizing aggregate properties within patches at high diversity[8]. Similarly, spatial variability of species composition, or beta-diversity, may create asynchrony of ecosystem properties among patches, stabilizing ecosystem properties at the metacommunity scale (see the conceptual diagram, Supplementary Fig. 1). Dispersal may decrease beta-diversity and spatial heterogeneity (Fig. 1b, Fig. 3b–d) and increase synchrony, potentially eliminating this stabilizing effect (Supplementary Fig. 1). In our experiment, grazer diversity did reduce synchrony of epiphyte abundance among patches, but only without dispersal (data not shown; see Supplementary Methods). This conceptually supports the spatial insurance hypothesis for metacommunities[15], but also demonstrates that diversity can contribute insurance through spatial variation even in the absence of dispersal.

The contrast between predicted stabilizing effects of diversity and dispersal, and our findings that diversity more often made ecosystem properties less predictable in space and time, highlights a potentially fundamental difference in processes mediating BD–EF relationships in single versus multitrophic ecosystems: the influence of active food and habitat selection by mobile consumers. At the metacommunity level, grazer dispersal eliminated the stabilizing effect of diversity on ecosystem properties (Fig. 3g, h), and at the patch level, grazer dispersal consistently increased temporal variability (Fig. 3e, f). Both results contradict the spatial insurance hypothesis, which is based on equilibrium metacommunities of sessile organisms with passive dispersal[15]. In communities of mobile animals, where dispersal is active and competitive exclusion is rare, connecting patches may allow both rapid recruitment to an optimal habitat and emigration after resource depletion, inflating temporal variability within a given patch and enhancing spatial heterogeneity. This hypothesis is also consistent with our finding that, at least in less diverse communities, dispersal enhanced grazer impacts on edible algae but reduced impacts on inedible algae (Fig. 2c, e). Habitat selection, then, might be a means by which species interactions, including those that mediate production, transcend the local scale and affect patterns at metacommunity scales[25,26].

Biodiversity-stability theory, like most ecological theory, assumes equilibrium[2,8–10,15]. Although our communities experienced colonization, extinction and reached carrying capacity, they probably did not reach compositional equilibrium. Therefore, the increased temporal variability we observed in response to both diversity and dispersal might be due to transient dynamics. In nature, however, grazer composition shifts, and seagrass patches change in size and location over timescales comparable to the length of our experiment, owing to seasonal dynamics and disturbances (K.E.F. and J.E.D., unpublished observation). Because such non-equilibrium phenomena are important in most natural ecosystems, we believe our results are broadly relevant. Furthermore, running the experiment for longer would probably increase the importance of dispersal, which eliminated the predicted and observed stabilizing effects of diversity (Fig. 3e–h). Consequently, our results probably differed from diversity-stability predictions because we used mobile consumers that can actively choose patches and affect spatial heterogeneity of resources, rather than sessile organisms with passive dispersal.

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Our experiment demonstrates that the stabilizing effect of biodiversity can be modified by both dispersal and scale, supporting previous theory and empirical research demonstrating that both dispersal and scale can modify the effect of biodiversity on the magnitude of productivity[14–17]. Furthermore, our results indicate that increasing diversity will not necessarily increase the predictability of ecosystem functioning in space as it often does in time. There may be tradeoffs, then, between maximizing diversity across landscapes and stabilizing ecosystem services in time. However, our experiment also corroborates—for the first time—theory predicting that diversity can enhance reliability of ecosystem services through a spatial mechanism[15]: spatial heterogeneity created by more diverse metacommunities of grazers stabilized ecosystem properties at the metacommunity scale. Clearly, the spatial and temporal processes that influence diversity within natural landscapes can substantially influence the ways that biodiversity mediates ecosystem functioning. Integrating these influences is critical to effective management of ecosystem services in response to habitat fragmentation and other drivers of biodiversity change.

METHODS

Experimental organisms. *Z. marina* (eelgrass) is the most widespread and abundant marine macrophyte in the Northern Hemisphere, and it supports many commercially important species[27]. The dominant primary consumers in many eelgrass beds are small crustacean grazers, which feed on epiphytic algae and can have important indirect, positive effects on eelgrass[27]. We manipulated diversity of these grazers, which all have overlapping generations, direct development and summer generation times of 3–4 weeks.

Mesocosm system. The experiment was conducted in outdoor, flow-through 13.5-litre eelgrass mesocosms. Filtered seawater from the York River estuary, Virginia, USA, was delivered in pulses to mesocosms shaded to approximate natural light levels. Fifteen pre-weighed *Z. marina* shoots were planted in each mesocosm. Filters excluded grazers, but allowed passage of propagules of other invertebrates and algae[28,29]. We grouped mesocosms into metacommunities consisting of five patches (individual mesocosms) each. For half of the 20 metacommunities, patches within the metacommunity were connected to a central hub via clear vinyl tubing with a 2.2-cm internal diameter. These dispersal corridors were 5 cm long, so grazers had an equal chance of dispersing to all other patches within the metacommunity. All grazer species could swim rapidly through the dispersal corridors, but dispersal between patches was relatively infrequent, and species differed in their dispersal inclinations (Supplementary Table S1). There was no active dispersal between unconnected patches, but these patches were linked into a metacommunity by sharing a common water supply, which was the source of propagules of all species other than the manipulated grazers.

Experimental design. We used a fully-crossed, two-factor analysis of variance (ANOVA) design with metacommunity richness and dispersal as the two factors. Metacommunity richness had two levels, low (three spp.) and high (eight spp.). The low-richness species pool was a subset of the high-richness species pool, consisting of the three most abundant grazers in the field at the time of the experiment (Supplementary Table S4). The high-richness pool included approximately 75% of the crustacean grazer species known from the lower Chesapeake Bay region (Supplementary Table S4). Each treatment combination (metacommunity richness × dispersal) was replicated five times. The initial grazer community inoculated into each mesocosm was 15 reproductively mature male–female pairs, the species composition of which was determined by random draws of pairs of individuals from the designated species pool (Supplementary Table S4). Each metacommunity initially contained the full complement of species from the whole pool, but most individual mesocosms did not. The experiment ran for 47 days, long enough for at least two complete generations of most species in addition to the founding generation, population increases approaching two orders of magnitude, and achievement of carrying capacity[29,30].

Sampling ecosystem properties. At two-week intervals, we estimated the biomass of epiphytic algae as epiphytic chlorophyll[28]. Mid-way through the experiment (day 26), we sampled grazers by sweeping a dip net at mid-depth ten times, and counting and identifying the grazers captured. We estimated spatial variability of ecosystem properties as the coefficient of variation (c.v.) of each response variable across the five patches in a metacommunity. Spatial variability was initially zero, and resulted from a combination of random variation in colonization through the flow-through system and subsequent interactions with the grazer community. We also estimated temporal c.v. of epiphytic chlorophyll (three time points) and grazer abundance (two time points). At the end of the experiment, all organisms retained by a 0.5-mm mesh sieve were separated, identified, dried to constant mass, ashed at 450 °C, and massed again.

Statistical analyses. To determine whether dispersal erased the signature of initial composition, we analysed the relationship between initial and final relative abundance for each species using a General Linear Model (GLM) with dispersal as a class predictor (Supplementary Table S1). For response variables measured within patches, we analysed data using a GLM with three factors: grazer metacommunity richness and dispersal, which were fully crossed, and metacommunity identification number (ID), which was nested within the fully-crossed design. When the *P*-value for metacommunity ID was >0.25, we ignored that factor and ran a fully-crossed, two-way ANOVA with metacommunity richness and dispersal ($n = 25$). For response variables determined at the metacommunity level, data were analysed using a fully factorial, two-way ANOVA with metacommunity richness and dispersal as the factors ($n = 5$). We also analysed the relationship between final grazer diversity and ecosystem properties using a GLM with final Shannon–Weaver (S–W) diversity of grazers as a continuous predictor and dispersal as a class predictor. Patch S–W was used for responses in patches, and metacommunity S–W was used for metacommunity responses and spatial heterogeneity.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions K.E.F. planned and executed the experiment and wrote the manuscript. J.E.D. contributed to the planning and writing process.

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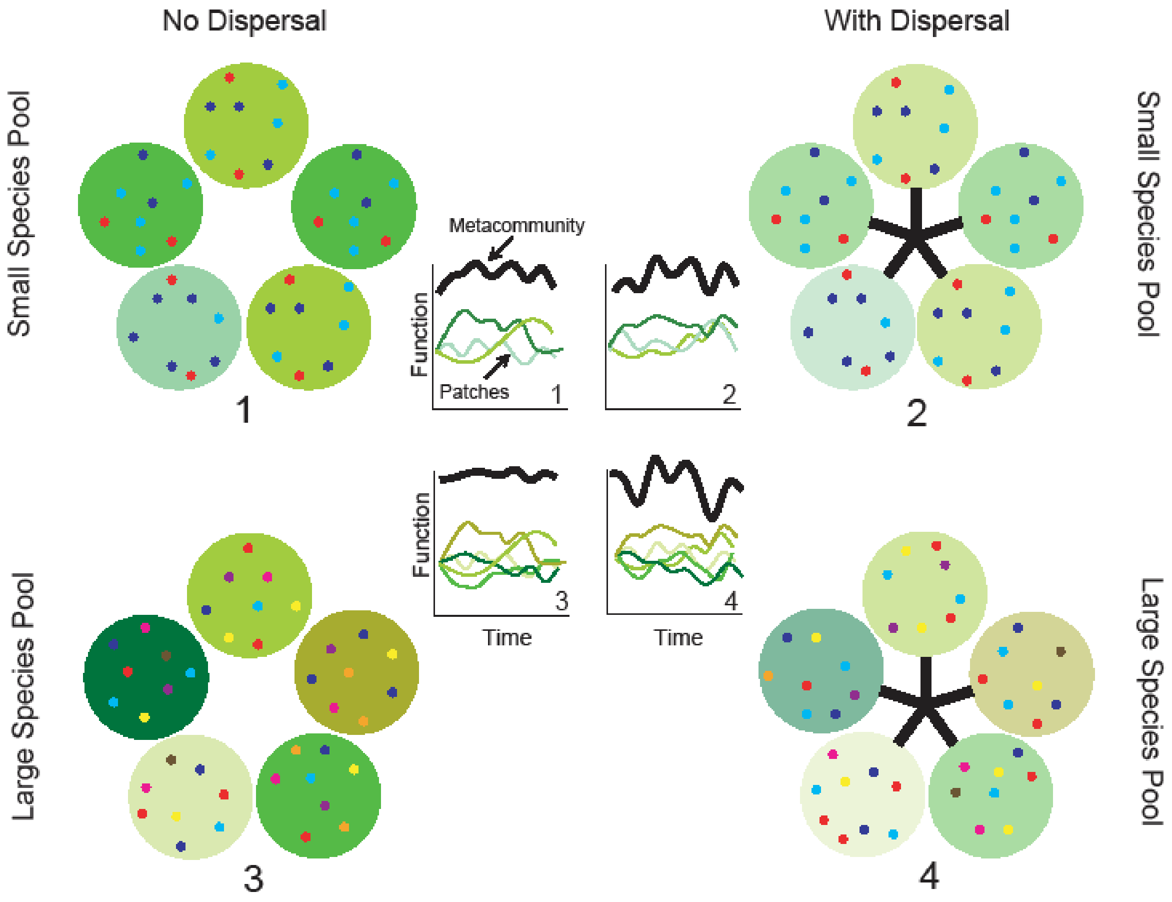

Supplemental Figure 1: Conceptual diagram of effects of species pool size and dispersal on spatial and temporal variability of ecosystem properties. Large circles represent patches, and each cluster of five patches is a metacommunity. Small circles within the patches represent individual grazers; colors signify species. Each combination of grazers consumes resources differently, creating spatial heterogeneity, as shown by the contrast between patch colors within a metacommunity. Patches of the same color are similar in species composition and grazing efficiency; consequently they have the same temporal fluctuations and are shown by the same color line on the graphs. Graphs show the fluctuations through time of a hypothetical ecosystem function, such as primary productivity, within each patch (thin lines, color matches patch color) and within the metacommunity as a whole (thick line, summed function of individual patches).

Increasing the number of species in the species pool used to assemble metacommunities leads to greater spatial variability in grazer species composition, which enhances spatial heterogeneity of the grazers' resources and the variety of temporal patch trajectories. This greater variety of patch trajectories stabilizes metacommunity function through time.

Dispersal decreases spatial variability and increases synchrony (temporal fluctuations in graphs are more in phase). This eliminates the stabilizing effect of metacommunity richness.

Supplemental Methods:

Selection effects. To determine whether effects of grazer metacommunity richness were due to the presence of a particular grazer species, we ran backwards elimination multiple regressions of each response variable against the final abundance of each grazer species. Backwards elimination regression showed that different combinations of species were significant contributors to the decrease in each food resource (Fig. 2); there was not a single species or a single combination of species that significantly explained all effects. Furthermore, the effects of metacommunity richness could not be explained simply by the presence of additional species in the high richness metacommunities; species also present in the low richness metacommunities contributed to all of the diversity effects observed. Species that were significant contributors to the spatial heterogeneity of algal, invertebrate, and *Z. marina* biomass were also not the same species responsible for the increase in beta-diversity.

Diversity measures. Beta-diversity was calculated as: Beta-diversity = 1 – (UV/(U+V+UV)) where U is the relative abundance of the shared species in patch 1 and V is the relative abundance of the shared species in patch 2[1]. Beta diversity was calculated for every possible pair of patches in a metacommunity and the mean was used as the datum from that metacommunity in the analyses.

Synchrony. Synchrony was calculated as the sum of the covariances of epiphyte abundance through time for each possible pair of patches within a metacommunity[2,3]. To determine whether or not diversity and dispersal affected synchrony, we used these summed covariances as the response variable in a GLM with S-W diversity as a continuous predictor and dispersal as a class predictor. Results are not shown, but synchrony marginally significantly decreased with diversity in unconnected communities, and dispersal increased synchrony.

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Supplementary Table 1 (Table S1): Effects of dispersal on extinction, colonization, and final composition compared with initial composition. Extinctions were instances where initial abundance was >0 and final abundance was 0; colonizations were instances where initial patch abundance was 0 and final abundance was >0. Comparisons of initial and final relative abundances of each species were made using a GLM with initial relative abundance as a continuous predictor and dispersal as a class predictor. Table cells are (F-statistic, p-value).

	Extinction rate		**Colonization rate**	**R2**	**F, p-value**			
Species	**No Disp**	**W/ Disp**	**W/ Disp**		**Initial Composition**	**Dispersal**	**Comp *Disp**	**Overall**
Erichsonella attenuata	0.38	0.45	0.2	0.3037	**9.97, 0.0028**	2.21, 0.1438	**5.92, 0.0189**	**6.69, 0.0008**
Gammarus mucronatus	0	0	1	0.4625	**28.35, <0.0001**	2.99, 0.0907	1.63, 0.2082	**13.19, <0.0001**
Idotea baltica	0.08	0.09	0.67	0.208	**7.27, 0.0098**	0.59, 0.4471	**8.30, 0.0060**	**4.27, 0.0096**
Ampithoe valida	0	0.05	0.4	0.1238	**6.04, 0.0178**	0.15, 0.7046	0.53, 0.4692	2.17, 0.1048
Cymadusa compta	0	0	1	0.4073	**21.01, <0.0001**	1.31, 0.2585	**5.23, 0.0268**	**10.54, <0.0001**
Dulichiella appendiculata	0.11	0.21	0.75	0.2516	**13.09, 0.0007**	0.15, 0.7047	1.26, 0.2676	**5.15, 0.0037**
Elasmopus levis	0.22	0.17	1	0.1407	**7.42, 0.0091**	0.50, 0.4851	0.64, 0.4295	**2.51, 0.0703**
Paracerceis caudata	0.67	0.85	0	0.0457	1.48, 0.2300	0.28, 0.6023	0.60, 0.4422	0.79, 0.5082

Supplementary Table 2 (Table S2): Effects of metacommunity richness and dispersal on patterns of diversity and ecosystem properties within patches and metacommunities. Data were analyzed using a GLM. Metacommunity ID is fully nested within the interaction term. When the p-value for it exceeded 0.2, we removed it from the analysis, changing the model d.o.f. from 7 to 3. Table cells are (F-statistic, p-value). When data were not normally distributed, they were log-transformed.

Response Variable	**Metacommunity Richness (df=1)**	**Dispersal (df=1)**	**Metacomm. Richness * Dispersal (df=1)**	**Meta-community ID (df=4)**	**Total (df=7,3)**
Patch (n=25 for each combination of treatments, n=100 total)					
Grazer species richness	**64.93, <0.0001**	0.9, 0.3441	**3.2, 0.0768**	4.05, 0.0045	**29.08, <0.0001**
Grazer Shannon-Weaver diversity	**700.19, <0.0001**	1.05, 0.3090	1.49, 0.2257	NS	**234.69, <0.0001**
Log grazer abundance	**24.05, <0.0001**	0.10, 0.7568	0.92, 0.3391	4.08, 0.0044	**5.99, <0.0001**
Epiphytic chl *a* (week 2)	**33.44, <0.0001**	**10.93, 0.0014**	**3.61, 0.0604**	7.53, <0.0001	**7.48, <0.0001**
Epiphytic chl a (week 4)	0.24, 0.6227	**4.02, 0.0477**	0.1, 0.7532	NS	1.46, 0.2317
Epiphytic chl *a* (week 6)	0.14, 0.7130	0.53, 0.4695	1.59, 0.2108	NS	0.76, 0.5219
Log total algal biomass	**20.91, <0.0001**	0, 0.9482	1.0, 0.3197	NS	**7.3, 0.0002**
Edible algae biomass (macroalgae)	**7.65, 0.0068**	1.29, 0.2583	0.75, 0.3874		**3.23, 0.0258**
Inedible algae biomass (cyanobacteria)	**4.85, 0.0301**	0.28, 0.6011	**3.17, 0.0781**	NS	**2.76, 0.0461**
Z. marina biomass	**19.05, <0.0001**	**4.98, 0.0280**	1.93, 0.1682	NS	**8.65, <0.0001**
Invertebrate biomass	**38.16, <0.0001**	1.87, 0.1752	0.09, .7637	NS	**13.37, <0.0001**
Log *M. manhattensis* biomass	**10.93, 0.0014**	**6.96, 0.0098**	**8.52, 0.0044**	3.51, 0.0104	**7.42, <0.0001**
Temporal CV of grazer abundance	**4.56, 0.0397**	1.44, 0.2386	0.63, 0.4308	NS	2.21, 0.1039
Temporal CV of epiphytic chl *a*	0.14, 0.7107	**11.31, 0.0011**	1.89, 0.1726	1.64, 0.1708	**2.00, 0.0629**
Metacommunity (n=5 for each combination of treatments, n=20 total)					
Grazer species richness	**77.04, <0.0001**	1.04, 0.3226	0.04, 0.8408	N/A	**26.04, <0.0001**
Grazer Shannon-Weaver diversity	**647.44, <0.0001**	**5.95, 0.0267**	0.24, 0.6333	N/A	**217.88, <0.0001**
Grazer beta-diversity	**4.94, 0.0411**	**3.39, 0.0844**	0.15, 0.7063	N/A	**2.82, 0.0720**
Grazer abundance	**19.78, 0.0004**	0.05, 0.8305	**3.73, 0.0715**	N/A	**7.85, 0.0019**
Total algal biomass	**9.91, 0.0062**	0.08, 0.7828	0.61, 0.4477	N/A	**3.53, 0.0390**
Edible algae biomass (macroalgae)	**4.96, 0.0406**	0.84, 0.3731	0.49, 0.4942	N/A	2.10, 0.1408
Inedible algae biomass (cyanobacteria)	**4.43, 0.0514**	0.25, 0.6227	2.90, 0.1078	N/A	2.53, 0.094
Z. marina biomass	**17.69, 0.0007**	**4.62, 0.0472**	1.79, 0.1997	N/A	**8.03, 0.0017**
Invertebrate biomass	**27.06, <0.0001**	1.32, 0.2670	0.06, 0.8028	N/A	**9.48. 0.0008**
M. manhattensis biomass	**67.71, <0.0001**	1.68, 0.2129	**3.42, 0.0831**	N/A	**24.27, <0.0001**
Spatial CV of grazer abundance	0.01, 0.9239	1.67, 0.2147	1.96, 0.1811	N/A	1.21, 0.3377
Spatial CV of epiphytic chl *a* (week 2)	1.32, 0.2683	2.42, 0.1397	0.30, 0.5904	N/A	1.34, 0.2952
Spatial CV of epiphytic chl a (week 4)	0.39, 0.5418	0.46, 0.5088	0, 0.9776	N/A	0.28, 0.8376
Spatial CV of epiphytic chl *a* (week 6)	0.02, 0.8841	0.79, 0.3879	1.5, 0.2388	N/A	0.77, 0.5281
Spatial CV of total algal biomass	**10.38, 0.0053**	1.31, 0.2688	0.24, 0.6318	N/A	**3.98, 0.0270**
Spatial CV of edible algae biomass	**3.67, 0.0736**	**3.44, 0.0820**	0.03, 0.8564	N/A	2.38, 0.1078
Spatial CV of inedible algae biomass	**8.80, 0.0091**	1.84, 0.1937	0.79, 0.3884	N/A	**3.81, 0.0310**
Spatial CV of *Z. marina* biomass	1.68, 0.2128	1.29, 0.2732	0.74, 0.4016	N/A	1.24, 0.3287
Spatial CV of invertebrate biomass	**4.17, 0.0581**	0.8, 0.3843	1.63, 0.2201	N/A	2.2, 0.1279
Spatial CV of *M. manhattensis* biomass	**21.65, 0.0003**	3.01, 0.1020	0, 0.9468	N/A	**8.22, 0.0015**
Temporal CV of grazer abundance	1.25, 0.3262	0.91, 0.3943	**10.34, 0.0324**	N/A	4.17, 0.1009
Temporal CV of epiphytic chl *a*	1.42, 0.2502	0.31, 0.5863	**3.07, 0.0991**	N/A	1.60, 0.2288

Supplementary Table 3 (Table S3): Effects of final grazer diversity on ecosystem properties at both patch- and metacommunity- scales. Data were analyzed using a GLM with grazer Shannon-Weaver (S-W) diversity as a continuous predictor and dispersal as a class predictor. Local response variables were regressed against local grazer S-W and metacommunity response variables were regressed against metacommunity S-W. Table cells are (F-statistic, p-value).

Response Variable	**Grazer S-W (df=1)**	**Dispersal (df=1)**	**Grazer S-W * Dispersal (df=1)**	**R2**	**Total (df=3)**
Patch (n=100)					
Grazer abundance	**19.30, <0.0001**	**3.52, 0.0638**	**4.52, 0.0361**	0.189	**7.37, 0.0002**
Log total algal biomass	**16.18, 0.0001**	0.33, 0.5669	0.69, 0.4083	0.156	**5.92, 0.0010**
Edible algae biomass (macroalgae)	**3.67, 0.0585**	1.87, 0.1861	0.42, 0.5183	0.054	1.82, 0.1496
Inedible algae biomass (cyanobacteria)	**3.80, 0.0542**	2.48. 0.1184	2.67, 0.1059	0.073	**2.51, 0.0634**
Z. marina biomass	**12.92, 0.0005**	0.19, 0.6653	1.53, 0.2197	0.175	**6.73, 0.0004**
Invertebrate biomass	**24.68, <0.0001**	0.84, 0.3624	0.03, 0.8537	0.224	**9.13, <0.0001**
Log *M. manhattensis* biomass	**19.24, <0.0001**	0.31, 0.5811	0.28, 0.5979	0.168	**6.42, 0.0005**
Temporal CV of grazer abundance	2.43, 0.1279	0.10, 0.7499	0.27, 0.6086	0.101	1.34, 0.2753
Temporal CV of epiphytic chl *a*	0.17, 0.6849	0.85, 0.3579	0.72, 0.3980	0.168	2.57, 0.0591
Metacommunity (n=20)					
Grazer abundance	**20.57, 0.0003**	**3.51, 0.0795**	**3.50, 0.0798**	0.601	**8.04, 0.00017**
Algal biomass	**9.50, 0.0071**	0.03, 0.8718	0.42, 0.5266	0.382	**3.29, 0.0478**
Edible algae biomass (macroalgae)	0.63, 0.4369	**3.46, 0.0812**	0.35, 0.5649	0.269	1.96, 0.1608
Inedible algae biomass (cyanobacteria)	0.54, 0.4723	0.08, 0.7862	**3.64, 0.0745**	0.350	2.87, 0.0688
Z. marina biomass	**18.34, 0.0006**	**4.41, 0.052**	1.69, 0.2120	0.603	**8.12, 0.0016**
Invertebrate biomass	**24.83, 0.0001**	0.40, 0.5347	0.09, 0.7668	0.620	**8.70, 0.0012**
M. manhattensis biomass	**48.11, <0.0001**	**5.31, 0.0350**	2.32, 0.1472	0.766	**17.48, <0.0001**
Spatial CV of grazer abundance	0.01, 0.9255	0.05, 0.8176	1.68, 0.2137	0.172	1.11, 0.3750
Spatial CV of epiphytic chl *a* (week 2)	3.17, 0.0941	0.00, 0.9749	0.49, 0.4920	0.287	2.15, 0.1138
Spatial CV of epiphytic chl a (week 4)	0.04, 0.8456	0.00, 0.9722	1.41, 0.2530	0.226	1.55, 0.2391
Spatial CV of epiphytic chl *a* (week 6)	0.00, 0.9682	1.02, 0.3282	1.15, 0.2499	0.072	0.41, 0.7472
Spatial CV of total algal biomass	**8.44, 0.0103**	0.41, 0.5313	0.03, 0.8649	0.376	**3.22, 0.0510**
Spatial CV of *Z. marina* biomass	0.06, 0.8080	2.31, 0.1484	1.02, 0.3278	0.535	**6.13, 0.0056**
Spatial CV of invertebrate biomass	**3.16, 0.0946**	1.12, 0.306	0.65, 0.4303	0.218	1.48, 0.2569
Spatial CV of *M. manhattensis* biomass	**17.38, 0.0007**	0.52, 0.4816	0.00, 0.9628	0.557	**6.70, 0.0039**
Temporal CV of grazer abundance	0.32, 0.6036	**6.19, 0.0676**	**5.94, 0.0714**	0.651	2.49, 0.1994
Temporal CV of epiphytic chl *a*	1.12, 0.3063	1.06, 0.3179	2.72, 0.1184	0.210	1.42, 0.2741

Supplementary Table 4 (Table S4): Initial patch and metacommunity composition. Cells are numbers of male-female pairs.

			Large Species Pool											
			Small Species Pool											
Metacommunity ID	**Patch ID**	**Dispersal?**	***Gammarus mucronatus***	***Erichsonella attenuata***	***Idotea baltica***	***Ampithoe valida***	***Cymadusa compta***	***Dulichiella appendiculata***	***Elasmopus levis***	***Paracerceis caudata***	**Total # of Grazers**	**Initial Patch Richness**	**Initial Patch S-W Diversity**	**Initial Metacommunity S-W Diversity**
1	1		3	5	7	0	0	0	0	0	30	3	0.453	0.472
1	2		4	6	5	0	0	0	0	0	30	3	0.471	
1	3		9	2	4	0	0	0	0	0	30	3	0.403	
1	4		6	5	4	0	0	0	0	0	30	3	0.471	
1	5		8	6	1	0	0	0	0	0	30	3	0.383	
2	6		4	1	1	3	3	0	1	2	30	7	0.785	0.896
2	7		2	0	2	1	3	3	2	2	30	7	0.825	
2	8		1	1	2	1	2	2	3	3	30	8	0.865	
2	9		4	2	1	3	1	2	1	1	30	8	0.840	
2	10		0	2	2	2	2	2	2	3	30	7	0.840	
3	11	+	2	10	3	0	0	0	0	0	30	3	0.374	0.475
3	12	+	4	2	9	0	0	0	0	0	30	3	0.403	
3	13	+	7	4	4	0	0	0	0	0	30	3	0.461	
3	14	+	3	5	7	0	0	0	0	0	30	3	0.453	
3	15	+	6	5	4	0	0	0	0	0	30	3	0.471	
4	16	+	1	3	3	0	2	2	1	3	30	7	0.810	0.890
4	17	+	1	3	1	0	4	1	2	3	30	7	0.785	
4	18	+	1	1	3	1	2	0	3	4	30	7	0.785	
4	19	+	4	1	3	2	0	2	2	1	30	7	0.800	
4	20	+	2	0	2	2	3	3	2	1	30	7	0.825	
5	21	+	5	5	5	0	0	0	0	0	30	3	0.477	0.474
5	22	+	8	5	2	0	0	0	0	0	30	3	0.421	
5	23	+	6	4	5	0	0	0	0	0	30	3	0.471	
5	24	+	1	8	6	0	0	0	0	0	30	3	0.383	
5	25	+	6	6	3	0	0	0	0	0	30	3	0.458	
6	26	+	3	3	3	2	0	1	2	1	30	7	0.810	0.887
6	27	+	2	2	0	0	3	4	2	2	30	6	0.760	
6	28	+	2	0	3	2	1	4	2	1	30	7	0.800	
6	29	+	3	2	5	1	2	0	1	1	30	7	0.767	
6	30	+	2	3	2	1	2	3	0	2	30	7	0.825	
7	31		1	7	7	0	0	0	0	0	30	3	0.387	0.465
7	32		6	7	2	0	0	0	0	0	30	3	0.430	
7	33		8	6	1	0	0	0	0	0	30	3	0.383	
7	34		5	7	3	0	0	0	0	0	30	3	0.453	
7	35		9	2	4	0	0	0	0	0	30	3	0.403	
8	36		2	1	2	3	1	4	1	1	30	8	0.840	0.891
8	37		2	3	2	1	2	2	2	1	30	8	0.880	
8	38		0	3	2	2	1	2	1	4	30	7	0.800	
8	39		1	4	4	1	2	1	1	1	30	8	0.815	
8	40		2	2	1	2	2	2	1	3	30	8	0.880	
9	41	+	5	8	2	0	0	0	0	0	30	3	0.421	0.473
9	42	+	4	7	4	0	0	0	0	0	30	3	0.461	
9	43	+	6	5	4	0	0	0	0	0	30	3	0.471	
9	44	+	6	3	6	0	0	0	0	0	30	3	0.458	
9	45	+	7	4	4	0	0	0	0	0	30	3	0.461	
10	46		6	5	4	0	0	0	0	0	30	3	0.471	0.462
10	47		7	6	2	0	0	0	0	0	30	3	0.430	

10	48		5	8	2	0	0	0	0	0	30	3	0.421	
10	49		3	5	7	0	0	0	0	0	30	3	0.453	
10	50		4	9	2	0	0	0	0	0	30	3	0.403	
11	51	+	4	1	0	2	4	2	0	2	30	6	0.735	0.889
11	52	+	1	0	4	2	0	3	2	3	30	6	0.744	
11	53	+	0	0	1	4	3	3	2	2	30	6	0.744	
11	54	+	2	2	2	3	2	1	2	1	30	8	0.880	
11	55	+	2	2	3	2	1	3	2	0	30	7	0.825	0.879
12	56		1	1	3	1	0	5	1	3	30	7	0.752	
12	57		3	2	1	0	0	4	2	3	30	6	0.744	
12	58		2	4	1	1	1	1	3	2	30	8	0.840	
12	59		2	2	2	2	1	2	2	2	30	8	0.895	
12	60		0	2	2	2	2	1	4	2	30	7	0.815	
13	61		6	6	3	0	0	0	0	0	30	3	0.458	0.477
13	62		3	6	6	0	0	0	0	0	30	3	0.458	
13	63		4	4	7	0	0	0	0	0	30	3	0.461	
13	64		6	3	6	0	0	0	0	0	30	3	0.458	
13	65		5	7	3	0	0	0	0	0	30	3	0.453	
14	66	+	2	2	3	1	0	1	3	3	30	7	0.810	0.881
14	67	+	3	2	3	1	2	3	1	0	30	7	0.810	
14	68	+	1	2	6	2	0	0	2	2	30	6	0.704	
14	69	+	4	1	1	0	3	1	5	0	30	6	0.687	
14	70	+	3	4	0	2	1	2	1	2	30	7	0.800	
15	71	+	5	8	2	0	0	0	0	0	30	3	0.421	0.469
15	72	+	5	8	2	0	0	0	0	0	30	3	0.421	
15	73	+	5	4	6	0	0	0	0	0	30	3	0.471	
15	74	+	6	5	4	0	0	0	0	0	30	3	0.471	
15	75	+	4	6	5	0	0	0	0	0	30	3	0.471	
16	76		1	5	1	3	1	0	1	3	30	7	0.752	0.893
16	77		1	3	0	1	4	3	2	1	30	7	0.810	
16	78		3	0	1	3	3	0	3	2	30	6	0.754	
16	79		4	1	3	1	1	1	2	2	30	8	0.840	
16	80		4	0	3	1	0	2	3	2	30	6	0.744	
17	81	+	6	5	4	0	0	0	0	0	30	3	0.471	0.474
17	82	+	5	5	5	0	0	0	0	0	30	3	0.477	
17	83	+	8	3	4	0	0	0	0	0	30	3	0.438	
17	84	+	4	8	3	0	0	0	0	0	30	3	0.438	
17	85	+	5	5	5	0	0	0	0	0	30	3	0.477	
18	86		3	0	3	2	0	2	1	4	30	6	0.744	0.879
18	87		2	1	5	1	0	1	2	3	30	7	0.767	
18	88		1	1	4	0	2	4	2	1	30	7	0.775	
18	89		0	3	2	2	3	3	2	0	30	6	0.769	
18	90		1	2	2	2	3	4	1	0	30	7	0.800	
19	91		4	4	7	0	0	0	0	0	30	3	0.461	0.475
19	92		4	7	4	0	0	0	0	0	30	3	0.461	
19	93		5	6	4	0	0	0	0	0	30	3	0.471	
19	94		4	5	6	0	0	0	0	0	30	3	0.471	
19	95		9	5	1	0	0	0	0	0	30	3	0.371	
20	96	+	2	1	3	4	3	1	1	0	30	7	0.785	0.896
20	97	+	2	2	1	1	3	3	2	1	30	8	0.865	
20	98	+	3	0	3	1	2	2	3	1	30	7	0.810	
20	99	+	2	3	2	1	2	2	2	1	30	8	0.880	
20	100	+	2	1	3	0	5	2	2	0	30	6	0.727	