Plant feeding promotes diversification in the Crustacea

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About half of the world's animal species are arthropods associated with plants, and the ability to consume plant material has been proposed to be an important trait associated with the spectacular diversification of terrestrial insects. We review the phylogenetic distribution of plant feeding in the Crustacea, the other major group of arthropods that commonly consume plants, to estimate how often plant feeding has arisen and to test whether this dietary transition is associated with higher species numbers in extant clades. We present evidence that at least 31 lineages of marine, freshwater, and terrestrial crustaceans (including 64 families and 185 genera) have independently overcome the challenges of consuming plant material. These plant-feeding clades are, on average, 21-fold more speciose than their sister taxa, indicating that a shift in diet is associated with increased net rates of diversification. In contrast to herbivorous insects, most crustaceans have very broad diets, and the increased richness of taxa that include plants in their diet likely results from access to a novel resource base rather than host-associated divergence.

herbivory | crustaceans | diversification | speciation | arthropods

The origin of novel traits that allow species to use a previously unexploited resource is widely used as an explanation for the high species richness in certain lineages of life on Earth. The hypothesis that these traits can be used to explain the variation in species richness among clades in the tree of life has been a major focus of evolutionary biology over the past decades (1, 2). Some of the most influential studies of trait-mediated diversification have focused on the morphological and behavioral innovations that allow access to a novel food resource and, in particular, the evolution of herbivory (3). Feeding on plants has long been considered an "evolutionary hurdle" (4) because of the low protein content of plant material relative to animal tissues and the presence of chemical and physical barriers to digesting plant material. Overcoming those hurdles was central to early hypotheses that plant feeding has promoted the high diversity seen in herbivorous insects (5). Formal tests of this hypothesis provided evidence that the shift to feeding on plant tissue is associated with higher species richness among the highly speciose orders of herbivorous insects (6) and with increased diversification in other organisms, including mammals (7) and dinosaurs (8).

The diversification of insects, in particular, once they began feeding on plant material, is thought to have given rise to much of the biological diversity on Earth today (9, 10), and there is an extensive literature that uses phylogenetic approaches to study the interaction between insect herbivores and their host plants (reviewed in refs. 11, 12). Increased diversity in the butterflies has been associated with shifts to feeding on more speciose plant groups (e.g., ref. 13) and to feeding on chemically distinct host plants (e.g., refs. 14 and 15). Among the beetles, the shift to feeding on angiosperms from the species-poor gymnosperms was associated with an increase in species richness by several orders of magnitude, leading Farrell (16) to title his study "*Inordinate fondness: explained*" in reference to J. B. S. Haldane's well-known quote about the astounding diversity of beetles on Earth (17). More recent analyses, however, have found either that herbivory promotes insect diversification (18) or no evidence for herbivory per se promoting diversification among the beetles (19) and among all insects (3). Wiens et al. (20) showed that the degree to which herbivory can explain insect diversification rates varies among lineages, suggesting that the role of herbivory in promoting diversification will be best understood by the examination of a wide variety of plant-feeding taxa.

Here we test whether consuming live plant and macroalgal tissues is associated with higher species richness in the Crustacea, the other major group of arthropods that commonly consumes plant material (Fig. 1) and the lineage from which insects are derived (18). Crustaceans are abundant, species rich, and ecologically diverse in most aquatic systems (21). Herbivorous and omnivorous crustaceans play an important role in ecosystem functioning (22) and can affect the growth and abundance of primary producers on rocky intertidal shores (23), in kelp forests (24), seagrass beds (25), salt marshes (26), mangroves (27), freshwater wetlands (28), and in tropical forests on land (29). Herbivorous amphipods and isopods are particularly abundant on aquatic macrophytes and have been likened to insects because of their feeding mode, use of host plants as both food and shelter, and interactions with producer secondary metabolites (30). In common with herbivorous insects in terrestrial systems, herbivorous crustaceans in many aquatic systems are a major component of secondary production and are an important link to higher trophic levels (31). Crustacean herbivores did not arise until after the Devonian period, and Vermeij and Lindberg (32) conservatively estimated that herbivory arose independently three times in the isopods, five times in amphipods, and four times in brachyuran crabs. This repeated and independent evolution of plant feeding among the Crustacea gives us an opportunity to test whether plant feeding is associated with higher species richness in clades that now include plant material in their diets.

In this study, we first provide a phylogenetic analysis of the distribution of plant feeding across all crustaceans and then use a sister-clade approach to test for shifts in species richness associated with plant feeding. We further test whether an evolutionary shift to plant feeding is associated with an increase in range size or geographic distribution. In general, niche breadth is positively

Significance

Understanding what morphological and behavioral traits promote the success of diverse groups of organisms is a major goal of evolutionary biology. The ability to consume novel food sources has been linked to the spectacular radiation of herbivorous insects that eat terrestrial plants on Earth. Among the crustaceans, the arthropod group that dominates aquatic environments, relatively few major taxa have overcome the challenges of consuming primary producers (plants and macroalgae). However, lineages that include plant material in their diets support more species than their most closely related lineages. The results of our analyses support the hypothesis that a shift in diet promotes speciation in this diverse and ecologically important animal group.

Fig. 1. Crustaceans that feed on plants and macroalgae include (A) amphipods (*Sunamphitoe femorata* living in nests on the giant kelp *Macrocystis pyrifera*; image: I. Hinojosa), (B) isopods (*Amphoroidea typa* consuming the kelp *Lessonia spicata*), (C) crabs (*Hemigrapsus crenulatus* grazing on intertidal green algae), and (D) crayfish that feed on freshwater macrophytes (*Pacifiastacus leniusculus*; image: T. Renals).

associated with range size (33), and some explanatory models of insect diversification on higher plants assume that a shift to a broader range of diets will involve an increase in range size (34). The analysis of the geographic distributions of plant-feeding crustaceans and their sister clade also allows us to test whether any observed patterns in diversity are confounded by sampling localities (e.g., herbivores being more likely to be found in species-rich regions).

Results

Prevalence of Plant Feeding in the Crustacea. Our review identified 185 genera from 64 families and five orders of marine, freshwater, and terrestrial Crustacea known to consume plant and macroalgal tissues (Table S1; detailed evidence for all genera is given in Dataset S1). Within each order, the number of plant-feeding taxa was a low proportion of the total number of genera and families (Table S1). Mapping the plant-feeding families onto available phylogenies (Fig. 2 and Fig. S1) provides a conservative estimate of 31 independent evolutionary transitions from a detritivorous and/or carnivorous diet to one that includes plant and macroalgal tissues (the most parsimonious hypothesized transitions are illustrated in Fig. S1).

Contrast of Species Richness in Plant-Feeding and Sister Clades. The species richness of plant-feeding clades was significantly greater than that of their sister clades, with the increase being 21-fold on average [mean ± SE: 21 ± 7.6, $P = 0.005$ with the diversity contrast test of Paradis (35), $n = 26$] (Fig. 3 and Table S2). Other statistical methods of comparing richness in sister contrasts gave similar results (Slowinski–Guyer test, $\chi^2 = 103$, $P < 0.001$; McConway–Sims test, $\chi^2 = 50.4$, $P = 0.002$). The higher richness in the plant-feeding clades remained when taxa known to feed only on macroalgae (i.e., that do not include angiosperms in their diet) were removed ($P = 0.005$, $n = 17$).

Although the plant-feeding clades were more frequently collected by biologists than their non–plant-feeding sister clades [more records per species in the Global Biodiversity Information Facility (GBIF) database, ratio t test, $t = 4.97$, $P < 0.01$] (Fig. 4A), the sister clades were very widely distributed (Fig. S2) and, on average, were very well represented in biological collections with a mean ± SE of 6,727 ± 1,827 records per clade in the Ocean Biogeographic Information

System (OBIS) database and 2,364 ± 986 records per clade in the GBIF database. The diversity contrast test was robust when the seven contrasts that include the taxa most likely to be data deficient (having fewer than 100 records in the OBIS or GBIF databases, $P = 0.023$) were removed and when increasing numbers of contrasts were removed at random. The median probability of resampled diversity contrast tests did not exceed 0.05 until 12 randomly selected contrasts were removed from the total of 26 (Fig. S3). Thus we consider our result robust to the identity of any single contrast or to the possibility that any single sister clade was falsely classified as not plant feeding because of limited knowledge about its diet.

Global Distributions of Plant-Feeding Clades. We detected no association between plant feeding and range sizes, estimated from the number of 1° latitude × 1° longitude blocks in which each species within each clade had been recorded in the GBIF database (ratio t test, $t = 0.51$, $P = 0.61$) (Fig. 4B). This result remains unchanged when considering estimates of range size at larger spatial scales (i.e., the number of 5° × 5° and 10° × 10° cells) (all t tests, $t < 1.2$, $P > 0.2$). The larger number of species in the plant-feeding clades resulted in these clades having a larger global distribution, occupying more 1° × 1° cells in the GBIF database (ratio t test, $t = 2.72$, $P = 0.01$) (Fig. S4B).

In both hemispheres the latitudes from which the plant-feeding and their sister clades are found broadly overlap (Fig. 4B). With
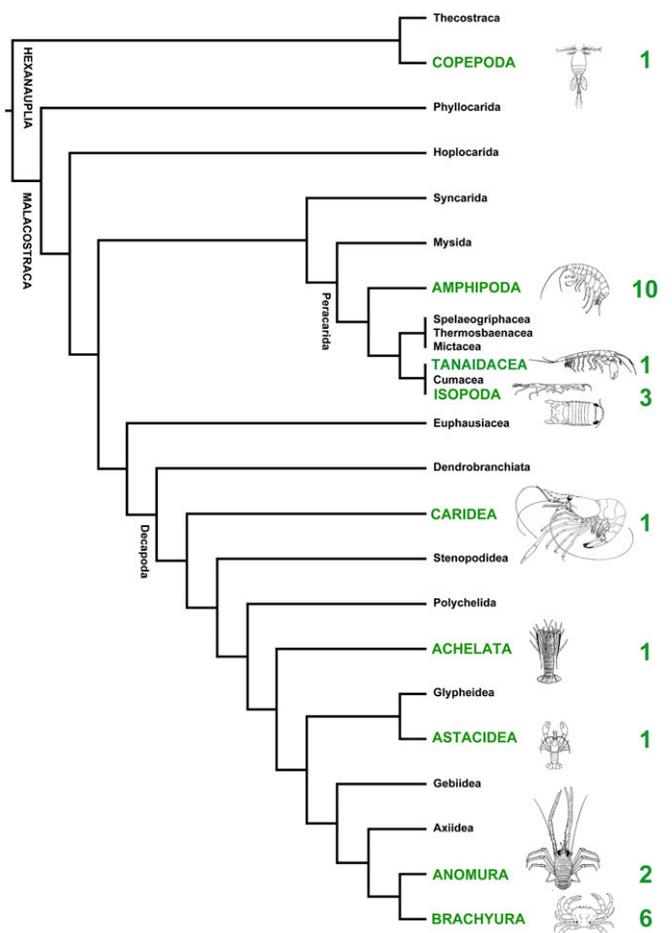
Fig. 2. Supertree of the Crustacea with major clades containing herbivores of macrophytes marked in green type and the minimum number of independent transitions to plant feeding (based on refs. 42, 74, and 75). The phylogenetic positions of transitions to plant feeding within these major crustacean taxa are illustrated in Fig. S1.
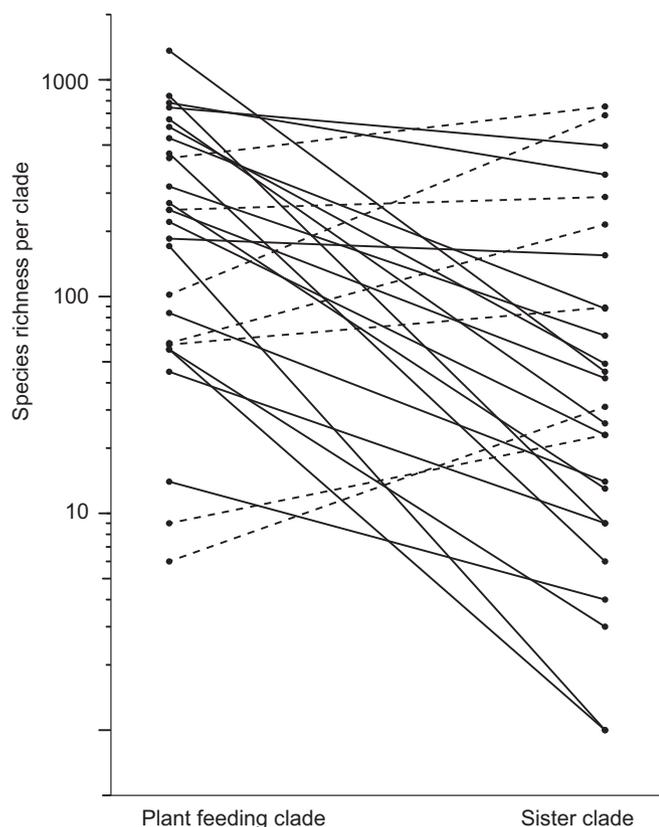
Fig. 3. Contrasts of species richness in plant-feeding and sister clades (*n* = 26, *P* = 0.005). The solid lines are the 19 contrasts with more species in the plant-feeding clade; the dashed lines are the seven contrasts with fewer species in the plant-feeding clade.

occurrence data from the GBIF database, we used the median of absolute latitude (i.e., degrees from the equator) for each species as a latitudinal midpoint, averaged these across all species within a clade, and used a standardized difference between these means (Hedge's *g*) for each pair of plant-feeding and sister clades. Combining all differences in a meta-analysis provided an estimate of an overall difference that did not differ from zero (95% CI: −0.04 to 0.77). We thus consider it unlikely that our contrast of diversity

between plant-feeding and their sister clades is confounded by any latitudinal patterns in the distribution of each clade type. For marine species, the plant-feeding and sister clades are widely distributed across biogeographic regions (Fig. S2), occurring on average in 8.3 of the 12 major realms defined by Spalding et al. (36). We detected no association between clade type (plant-feeding and their sister clades) and the number of contrasts within each biogeographic realm (χ^2 = 4.23, df = 11, *P* = 0.96).

Discussion

Marine, freshwater, and terrestrial crustaceans have repeatedly overcome the challenges of consuming plant material, and those plant-feeding taxa are, on average, 21-fold more speciose than their sister taxa, supporting the hypothesis that a shift in diet is associated with increased diversification.

Prevalence of Plant Feeding in Crustaceans. The phylogenetic distribution of plant-feeding crustacean taxa indicates that inclusion of plant material in the diet is a derived trait that has evolved multiple times from the ancestral diets of detritus and animal material. Our analyses with the latest available phylogenies suggest at least 31 independent evolutionary transitions from a detritivorous and/or carnivorous diet to a diet that incorporates live plant material, increasing the conservative estimate by Vermeij and Lindberg (32) of 12 times (three in the isopods, five in amphipods, and four in brachyuran crabs). Multiple independent transitions to plant-feeding diets also have been documented for other taxa, including insects (~25 origins of phytophagy in ref. 3), molluscs (32, 37), birds (38), and fish (39).

The concentration of plant feeding largely within three orders (of the more than 60 orders of extant Crustacea) is similar to the phylogenetic distribution of phytophagy in insects, in which it is found in relatively few orders (6). When considering all arthropods, the chelicerates and myriapods are primarily predators or scavengers, and within the crustacean clade [which includes insects (18)], consumption of multicellular primary producers is prominent only in the derived clades of the Hexapoda and Malacostraca. This paucity of plant-feeding clades supports the idea that the ability to consume plant material represents an evolutionary hurdle (4). The low proportion of major lineages that feed on macroalgae is not explained by lack of opportunity, with multicellular thalli present for ≈800 My and most marine herbivores (crustaceans, molluscs, echinoderms, and fish) arising only after the Paleozoic period (250 Mya) (32) but before the colonization of the sea by angiosperms ~100 Mya. Similarly, multicellular plants were present on land from
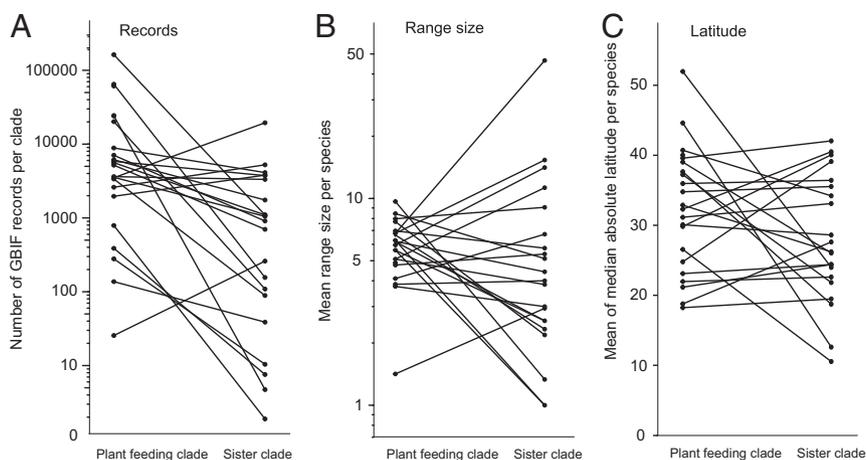
Fig. 4. Contrasts of plant-feeding and sister clades in (*A*) the number of records, (*B*) mean range size per species, and (*C*) mean of the median absolute latitude (degrees from the equator) of species from occurrence records in the GBIF database. Range size is the number of 1° latitude × 1° longitude blocks in which presence is recorded.

the Ordovician (470 Mya), whereas crustaceans did not colonize those habitats until much later [terrestrial amphipod, isopod, and crab fossils are known only from the Eocene (49 Mya) or later (40)]. Bousfield (41) estimated that most amphipod families had evolved by the Cretaceous, with both marine and freshwater groups presumed present in the Jurassic (150 Mya). Isopods and decapods are estimated to have diverged in the Ordovician–Silurian, although both groups do not attain the greatest diversity until the Mesozoic (42, 43). The actual timing of transitions to a diet including plant material is obviously more recent than the origin of the higher taxonomic groups considered here (44), so estimating the timing of these diet transitions will have to be inferred from time-calibrated phylogenies based on extant clades [as done recently for the amphipod family Gammaridae (45)].

Although there is an extensive literature examining the feeding biology of many crustaceans (Dataset S1), these reports are unevenly distributed among taxa, and the diets of most of the more than 67,000 species (46) are not known precisely (although much can be inferred from functional morphology). Uncertainty and variation in the diets of species within these clades and the possibility that diets of the sister clades are unknown have the potential to underestimate the number of times herbivory has arisen and either under- or overestimate the magnitude by which plant feeding has promoted diversity (3). There were relatively few families within our plant-feeding clades for which we found no evidence of plant feeding, but these families could have plant-, animal-, or detritus-based diets. Given our use of available phylogenies (many at the family level), there is certainly variation in feeding modes within the large groups we considered plant-feeding, both among species within the clade and within species, because many are omnivorous. We do not assume that every species within a plant-feeding clade includes plant material in its diet but conservatively estimate that there has been at least one transition to herbivory (or partial herbivory) in that clade.

Association Between Plant Feeding and Species Richness. Twenty-six independent sister comparisons provided clear evidence for higher species richness in the plant-feeding clades, supporting the hypothesis that plant feeding is an important trait that has promoted net diversification rates (i.e., speciation rates minus extinction rates). Similar tests with replicated contrasts of clades have shown that diversification can be promoted with the evolution of morphological traits, e.g., floral nectar spurs (47), ornamental traits involved in sexual selection (e.g., ref. 48), and traits that facilitate species interactions, e.g., defense mutualisms in plants (49), in addition to traits associated with dietary innovations.

The repeated transitions to plant feeding indicate selective advantages from exploiting plant material as a food source. Adaptive hypotheses to explain plant feeding, recently reviewed by Sanchez and Trexler (50), include intake efficiency (the use of a sedentary resource, often as both habitat and food, limiting the costs associated with finding mobile animal prey), the ability to inhabit areas with a high biomass of primary producers but few animal prey, the high lipid concentrations in algae, and a lower likelihood of disease transmission from parasites in animal prey. Despite the nutritional differences between macroalgae and angiosperms, most (19 of 26) plant-feeding clades in our review included both in their diets, and the diversity contrast remained robust when those that fed only on macroalgae were removed.

Plant consumption may favor increased diversification because plants represent a new adaptive zone (an abundant and diverse resource that was previously unavailable to consumers), coevolution of specialized herbivores with their host plants, and a "parasitic" lifestyle in which herbivores of limited mobility are more likely to have subdivided populations because of patchy distributions of their hosts (11). Of these competing, although not necessarily mutually exclusive, hypotheses, we consider the higher richness in plant-feeding crustaceans to be most likely explained by these animals having access

to a new adaptive zone with a more widespread resource base. This notion is consistent with the increased diversification in generalist mammalian herbivores accessing plant diets (7) and in three of four major clades of coral reef fish (Acanthuroidei, Chaetodontidae, Labridae, and Pomacentridae) when shifting to diets that include low-quality foods (algae, detritus, sponge, and corals) (39).

In stark contrast with herbivorous insects, plant-feeding crustaceans are almost all generalist consumers, able to consume material from many orders and several phyla of primary producers and also animal material and detritus when available (51, 52). Consequently, the mechanisms underlying host-associated divergence common in plant-feeding insects are unlikely to be important for plant-feeding crustaceans. The specialized and intimate associations between most insects and their hosts increases the likelihood of genetic linking between host use and mate choice and the likelihood that differences among populations will occur because of the patchy distribution of plants. Approximately half of speciation events among insects are estimated to be associated with shifts of specialized herbivores onto novel plant taxa (11, 34). However, the degree to which the initial transition to plant feeding has resulted in an increased diversification rate is unclear, with recent sister-clade comparisons failing to find any evidence for increased diversity among phytophagous beetles [eight contrasts (19)], and, for all insects, any effects of dietary ecology on species richness [26 contrasts (3)]. This finding contrasts with the positive association between plant feeding and species richness in the earlier influential study of Mitter et al. (6) using 13 sister contrasts across five orders of insects and with the more recent analyses of Wiens et al. (20) using phylogenetic generalized least-squares regression techniques.

The contrast of richness among sister clades is a powerful approach for testing hypotheses regarding diversification. It is important to note, however, that this approach is correlative (not causative), compares the net rate of cladogenesis (i.e., speciation minus extinction), and is sensitive to uncertainties in known sister relationships. We used recently available phylogenies for the Crustacea derived from both morphological and molecular data, but there is considerable uncertainty in the relationships among many higher taxa (44). With improved phylogenies that include both insects and the crustaceans from which they derived (18), there will be the opportunity to test further the role of feeding biology in the evolution of the Arthropoda. If the relationships among all taxa of interest are described within a single phylogeny, a series of more sophisticated analytical approaches to the sister-clade approach (including state-dependent speciation-minus-extinction models, e.g., ref. 53) or the more recent tests of Rabosky and Huang (54) could address the rates and timing of trait evolution.

Further differences between the plant–animal interactions of the largely aquatic crustaceans and the largely terrestrial insects also reduce the likelihood of host-associated divergence (51, 55) and may explain the lower global diversity of crustaceans as compared with insects. Given the central role of plant diversity in promoting insect diversity (13), the lower richness of aquatic primary producers [≈10,000 species of macroalgae in contrast to the ~300,000 species of plants (55)] is likely to limit the opportunities of host-associated divergence. The higher structural and chemical diversity within angiosperms offers more opportunities for herbivores to specialize on plant parts (e.g., stems vs. leaves vs. seeds and internal vs. external feeding). The parasitic lifestyle common among insects, in which individual herbivores often live on a single plant, is comparatively rare among crustaceans, because crustacean life spans commonly exceed that of their algal diet. Few species feed internally within macrophyte tissues (56), and there are no parallels with the diverse lineages of insects with piercing and sucking mouthparts. Finally, with a higher potential for dispersal and gene flow in an aquatic medium, localized distributions that would promote divergence are less likely. Unlike holometabolous insects in which oviposition behavior frequently

determines larval diets, most decapod crustaceans have dispersive larvae, and offspring habitats are decoupled from adult behavior [although brooding crustaceans (amphipods and isopods) could potentially place offspring on selected hosts (57)].

With few crustaceans having specialized diets, the evolutionary transition to plant feeding is, in most cases, a shift to a broader diet that includes plants in addition to other material. Expanded diets are predicted to promote greater local abundance and a larger range size and then net diversification through a greater probability of allopatric speciation (58). Our analyses contrasted the general pattern of larger range sizes with wider resource use (33, 59), with no evidence for difference in range sizes between plant-feeding and sister clades. The links between niche breadth and range size are complicated by sampling issues and the phylogenetic independence among sampling units (60). Our sister contrasts provide tests of range size that control for phylogeny, but variation in sampling effort, whereby widespread taxa are more likely be the focus of studies that document diets, has the potential to influence overall patterns. Although our dataset cannot entirely exclude this explanation, the sister clades in our analyses were themselves mostly higher taxa (families and family groups) with very broad geographic distributions (Fig. S2) and in many cases were the subject of large numbers of ecological studies that document animal or detrital diets.

The higher richness of plant-feeding clades also could arise from geographic patterns in species richness if either plant-feeding or sister clades were sampled disproportionately from regions with high richness. We consider confounding by uneven sampling unlikely, because neither the occurrence of clades within biogeographic realms nor mean latitudes differed between plant-feeding and their sister clades (Fig. 4), and there are no clear gradients of increasing crustacean richness with decreasing latitude (61).

Conclusions

The repeated, independent transitions to a diet that includes plants and/or macroalgae are associated with higher species richness in a diverse selection of aquatic and terrestrial crustaceans and support the hypothesis that feeding on plants has promoted diversification among animal consumers. Although few studies have examined the role of evolutionary history in crustacean diets, existing studies do indicate a strong phylogenetic signal for feeding behavior and ecology in herbivorous crustaceans (52, 59, 62) and among other grazers of aquatic macrophytes [e.g., opisthobranch molluscs (37) and fish (39)]. Promising avenues of research will include tests of how phylogeny explains the composition of plant diets, tests of morphological changes associated with diet shifts, contrasts between marine and freshwater systems in which crustaceans coexist with insect herbivores, and tests for associations between herbivore richness and the diversity of available plants.

Materials and Methods

Review of Plant Feeding in the Crustacea. From a literature search, we extracted a list of crustacean genera that include species known to feed on live, multicellular tissue from macroalgae and/or vascular plants [following the definition used by Mitter et al. (6) for plant-feeding insects and Vermeij and Lindberg (32) for marine herbivores]. The search terms and criteria for the evidence for plant feeding are detailed in the *SI Text*.

Contrast of Species Richness in Plant-Feeding and Sister Clades. We tested whether plant feeding is associated with higher species richness in the Crustacea by contrasting the number of species in the clades that include plant-feeding genera with the number of species in their sister clades. Clades were predominantly families or groups of families, given the taxonomic resolution of the most recently published phylogenies for higher-level taxa among the amphipods (63, 64), isopods (65, 66), and decapods (42, 67–69). The methods for determining which taxa to include in each sister contrast are detailed in the *SI Text*. This sister-clade approach has been widely used (35) and does not require a detailed fossil record (which is poor for many groups of crustaceans) or a complete phylogeny for the entire group in focus (currently unavailable for the Crustacea at the taxonomic resolution required). The approach has the advantage of including the independent, replicated contrasts needed to test whether the repeated evolution of a trait is associated with changes in species richness and to control for differences in diversity expected for clades of varying age (70).

We contrasted the species richness in plant-feeding and sister clades with the likelihood ratio test developed by Paradis (35) in the package 'ape' in R (71). For amphipods and isopods, the currently accepted taxonomy and number of species in each clade were established from the World Amphipoda Database (marinespecies.org/amphipoda) and the World List of Marine Freshwater and Terrestrial Isopod Crustaceans (marinespecies.org/isopoda). For tanaids, copepods, and decapods, we used the World Register of Marine Species (WoRMS; marinespecies.org), with the exception of freshwater crayfish, whose species numbers were taken from refs. 72 and 73. To test how robust our results were to the identity of individual taxa included in the sister comparisons, we repeated the analyses (*i*) with only taxa that consumed angiosperms, (*ii*) excluding poorly studied taxa that are likely to have undescribed diets, and (*iii*) with individual taxa randomly removed (details of these resampling methods are given in the *SI Text*).

Global Distributions of Plant-Feeding Clades. The global distributions of plant-feeding clades and their sister clades were contrasted (*i*) to test whether evolutionary shifts to plant feeding have facilitated increases in range size and (*ii*) to test the likelihood of our contrasts being confounded by possible regional differences in richness (latitude, biogeographic regions) or niche breadth [e.g., as varies with latitude in brachyuran crabs (59)]. Although declining species richness with increasing latitude is not the universal pattern among crustacean taxa (61), the potential exists for the plant-feeding clades to have been sampled disproportionately from regions with higher richness. We extracted the latitude and longitude of all available occurrence records for species within each clade from the GBIF (www.gbif.org/) and OBIS (www.iobis.org) databases. The methods for estimating range size and for contrasting range size, mean latitudes, and occurrence in biogeographic realms between plant-feeding and sister clades are detailed in the *SI Text*.

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