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Wild food portfolios: Access to diverse foods stabilizes harvest in wild food systems

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Wild foods are critical to the food security of billions of people worldwide, yet the ecological mechanisms that promote wild food system stability remain poorly understood. Within complex food webs, ecological theory predicts that nonhuman consumers can maintain more stable consumption rates by foraging on multiple resources that vary asynchronously in their availability across space and time. These so-called portfolio effects may also sustain more stable harvest rates by humans in wild food systems. We analyzed wild food harvest patterns for 46 isolated rural communities in southern coastal Alaska that harvest a diversity of wild foods (96 taxa) across terrestrial, freshwater, intertidal, and marine habitats. We show that access to diverse wild foods across this heterogeneous landscape dampened variability in harvest through time and increased robustness to species declines by allowing communities to harness seasonal and interannual asynchronies in wild food availability. These results demonstrate how ecological mechanisms that stabilize ecosystems may also underpin the stability of human wild food systems. Managing landscapes to maintain access to diverse wild foods and adopting flexible governance that allows communities to adjust harvest as patterns of wild food availability shift through time are crucial to sustaining resilient wild food systems in a changing world.

wild food systems | portfolio effects | stability | food system resilience | Alaska

Significance

Wild foods are essential to global food security, yet the mechanisms that stabilize these systems are poorly understood. Using harvest data from 46 rural communities in Alaska, we show that access to diverse species across habitats stabilizes harvest rates through time and increases robustness of harvest to species declines—mirroring portfolio effects that stabilize ecological communities. These results demonstrate that application of ecological theory can illuminate the dynamics of human food systems, and that maintaining access to diverse wild foods is crucial to the stability of wild food systems that support billions of people across the globe.

Wild foods are an important source of food for billions of people and are critical to global food security (1–5). While substantial research has focused on understanding the stability of cultivated or commercial food systems (6–9), factors that contribute to the stability of wild food systems have been understudied. This highlights a missed opportunity to further the global food systems agenda of improving food security, ending hunger and poverty, and building climate resilience (4). In a rapidly changing world, identifying mechanisms that promote wild food system stability and resilience is critical to sustainable wild food management and governance frameworks (2, 4, 5, 10). Here, we utilize an expansive wild food harvest database to examine how harvest patterns contribute to the stability of wild food systems in rural communities.

Consumption of wild foods has been linked to more diverse, nutrient-rich diets and lower rates of food insecurity (2, 11–14). In many regions of the world wild foods are often a primary source of essential micronutrients (11) and can contribute to large proportions of macronutrient consumption [e.g., 80% of protein consumed by local communities in the Congo Basin is obtained through bush meat (15); 90% of essential dietary fatty acids are obtained through wild foods in Arctic Alaska Native communities (16)]. Wild foods are particularly important at times of resource stress [e.g., drought periods (10, 11)] and in regions where healthy and nutrient-rich cultivated or store-bought foods are unavailable or too expensive (11, 17). For instance, many rural regions are not connected to reliable road systems, requiring store-bought foods to be shipped or flown in at great expense and infrequent intervals (18, 19). Harvesting wild foods is also critical to maintaining the cultural, spiritual, and economic ways of life for many people living in rural and Indigenous communities (2, 5, 20, 21).

Pervasive and ongoing threats such as climate change and land-use modification are rapidly altering the stability and function of ecosystems that provision wild foods (1, 2, 6, 22–25). In Arctic and sub-Arctic regions, for example, shifting environmental conditions (e.g., flow regimes, temperature, and ocean pH) are altering the availability and accessibility of important wild food species such as salmon, crab, and berries (23, 26, 27). Understanding the stability of these complex socioecological wild food systems in the face of such rapidly changing conditions requires development of both social and ecological theory (4). Recent advances in understanding wild food system stability from a socioeconomic perspective have highlighted the importance of social factors such as food (and knowledge) sharing networks within communities (28), economic factors such as the

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ability to purchase necessary supplies and equipment (e.g., vehicles, fuel) (29), and regulatory factors that restrict harvest (30). However, limited research has focused on developing ecological theory to understand how patterns of wild food harvest, such as the diversity of foods and habitats that contribute to wild harvest, promote stability (4, 5).

Wild food systems frequently encompass a diversity of wild foods harvested from different habitats and ecosystems (Fig. 1). For example, rural farming communities in Bangladesh harvest 102 species of greens from forests and 69 species of fish from rivers (31), and across China, wild plants and animals are gathered from a variety of environments surrounding agricultural landscapes such as forests, ponds, and irrigation ditches (32). Although there may be a few species that dominate overall harvest [e.g., salmon in many parts of Alaska (33)], other less-harvested species can contribute to food system stability by buffering against the decline of any single species. Additionally, the availability of different types of wild foods can vary over time (e.g., seasonally) and across different habitats (28, 34, 35), such that harvest strategies that focus on diverse food sources over multiple habitats may contribute to more consistent wild harvest [so-called portfolio effects (36)]. For example, Indigenous communities have a long history of utilizing a diverse array of species across heterogeneous landscapes to ensure a steady supply of food in variable environments (28, 37). Such harvest strategies can play a key role in maintaining stable harvest patterns through time and potentially contribute to the stability of harvested species. Thus, studies examining wild food system stability should capture the diversity of species and habitats that provision foods to communities.

Alaska provides a powerful context to study wild food system stability due to its heterogeneous landscapes that provision a diversity of wild foods critical to the well-being of rural and Indigenous communities. The coastal temperate rainforest in southern coastal Alaska, for instance, is a complex and interconnected landscape composed of terrestrial, freshwater, intertidal, and marine habitats supporting diverse wild foods that have sustained Alaska Native peoples (Xaad Kíl (Haida), Sm'algyax (Tsimshian), Lingít (Tlingit), Sugpiat (Alutiiq), Dena'ina, and dAXunhyuu (Eyak)) since time immemorial, and continue to sustain communities today (Fig. 1). However, rapidly shifting climate conditions in this region are challenging the resilience of these vital food systems (27, 28, 38). For example, drought-induced salmon mortalities (26), invasive species expansions (39), and harmful algal blooms (40) are constraining availability and access to key foods (27), while more frequent extreme weather, such as severe storms and flooding (41–43), are narrowing safe and favorable harvest windows, even for species expected to increase in abundance such as deer (27). Furthermore, wild food species and their habitats are managed by multiple federal, state, and Tribal agencies, creating regulatory complexities and competing priorities that further challenge accessibility (33). These overlapping pressures highlight the need to better understand the mechanisms that stabilize wild food harvest, and identify ecosystem management strategies that uphold rural and Indigenous ways of life amid accelerating environmental change.

Drawing from ecological theory, we develop and apply a framework to evaluate how harvest patterns influence harvest stability in wild food systems. Using wild harvest data from 46 rural communities in southern coastal Alaska where wild foods are critical to people's way of life (17), we ask: 1) what is the diversity and spatial distribution of wild food harvest (i.e., harvest structure)? and 2) how does this harvest structure influence harvest stability, both in terms of variability of harvest through time and robustness

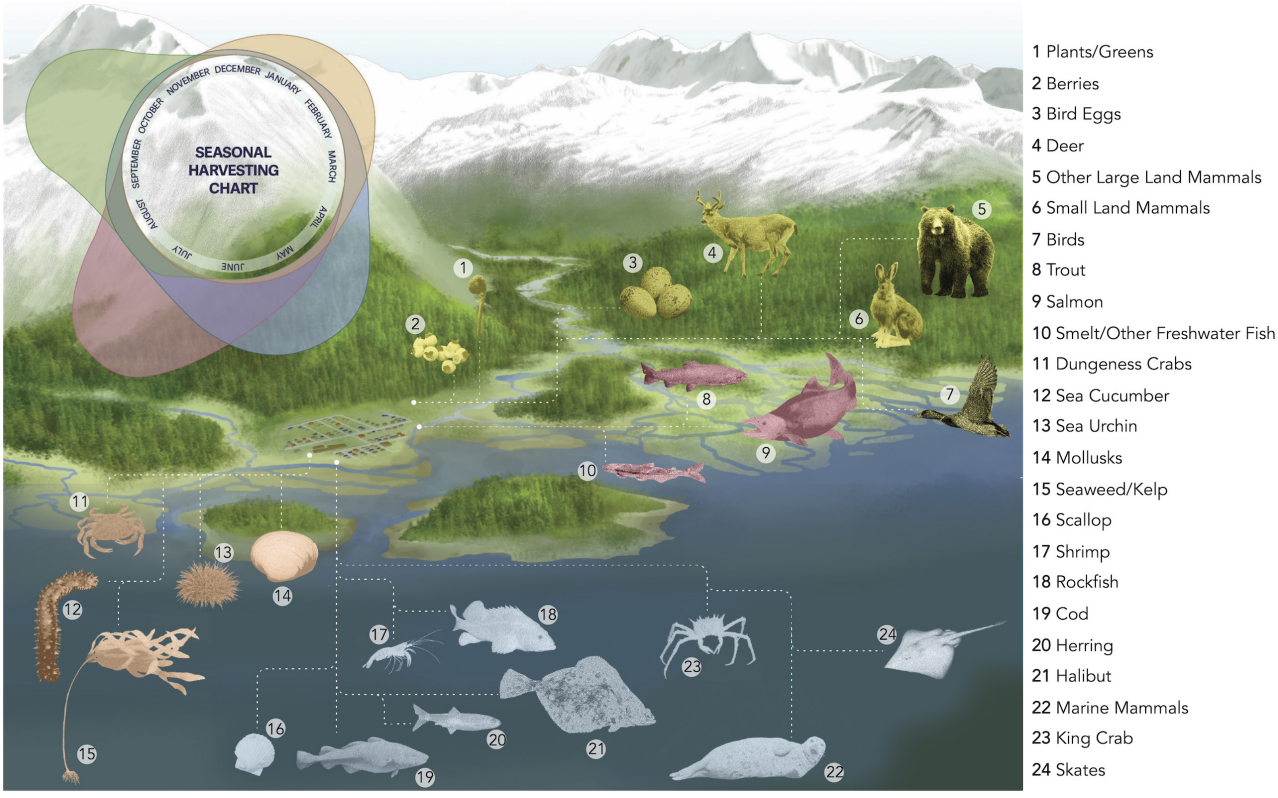

Fig. 1. Schematic of wild food systems in southern coastal Alaska. Communities harvest diverse wild foods across heterogeneous landscapes. Artwork by Cecil Howell.

to species loss? We show that access to diverse wild foods across multiple habitats enhances both harvest stability and robustness, extending ecological concepts of portfolio effects to human wild food systems. These findings highlight how maintaining (and restoring) access to diverse foods across heterogeneous landscapes, an approach deeply rooted in Indigenous and local knowledge systems (34, 37, 44) supports the capacity to provide sufficient, appropriate, and accessible food over time (45).

An Ecological Framework for Examining Wild Food System Structure and Stability

Within wild food systems, humans are intimately connected to the ecosystems they rely on for food and can be envisioned as predators or consumers within the food web they harvest from. The field of food web ecology has elucidated mechanisms that inform how the structure of food webs (i.e., whom eats whom and how much) relate to the stability (e.g., persistence, variability) of species within ecosystems (46–50). Here, we apply ecological concepts on the relationship between food web structure and stability to develop a framework for understanding how patterns of wild food harvest by human communities (i.e., harvest structure) influences the stability of wild harvest (Fig. 2). We calculate two harvest structure metrics that we hypothesize are linked to harvest stability, harvest diversity, and habitat coupling (Fig. 2 *B* and *C*). Below we define and develop hypotheses on how these two structural metrics contribute to harvest stability, in terms of both temporal harvest stability and harvest robustness to species loss (Fig. 2*D*).

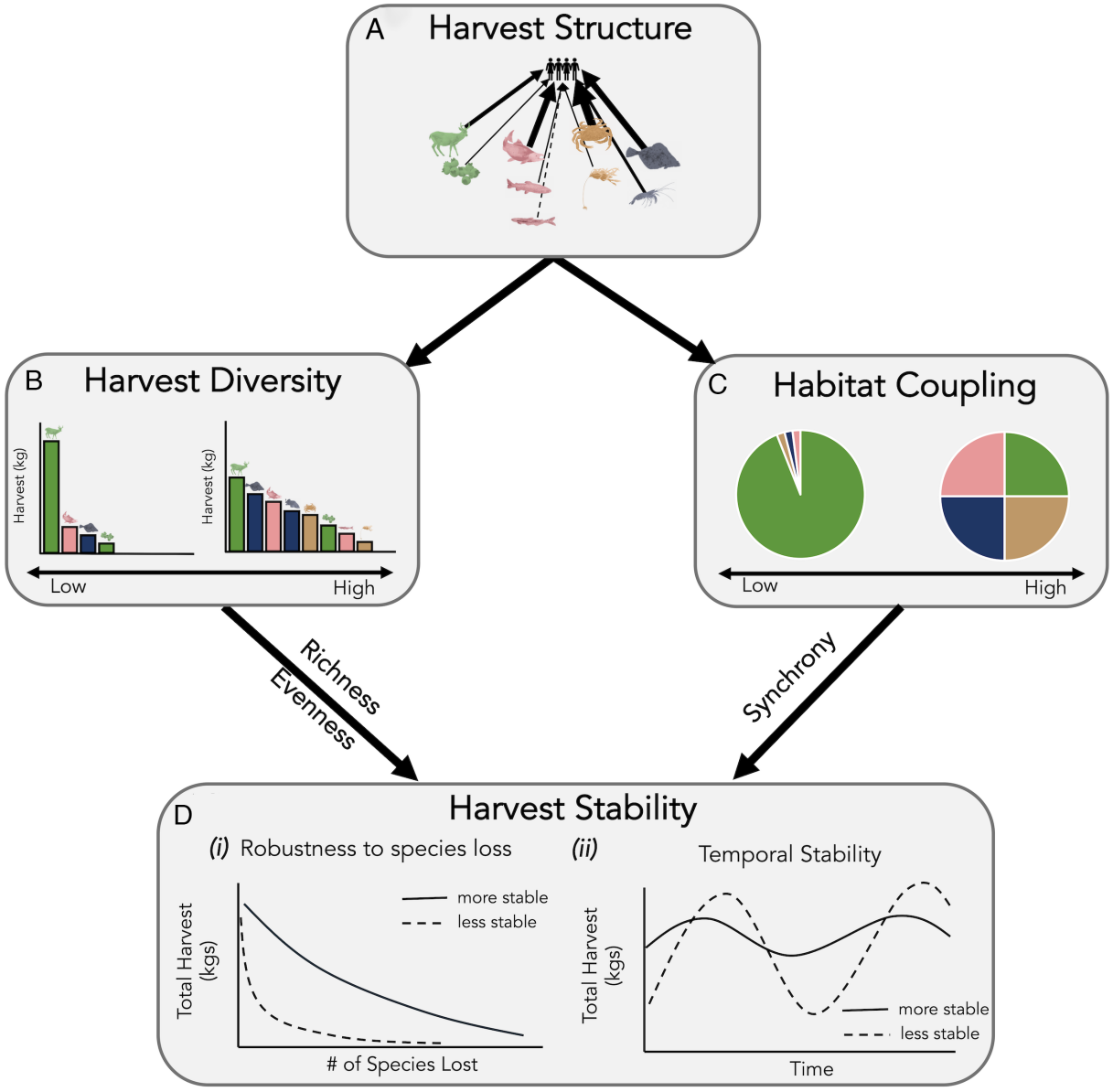

Fig. 2. Conceptual framework linking wild harvest structure to harvest stability. (*A*) simplified schematic of harvest structure, where color of species harvested represents habitat harvested from (terrestrial—green, freshwater—pink, intertidal—brown, marine—blue), thickness of arrows represent differences in harvest magnitude (per capita harvest). (*B*) communities exhibit gradient in harvest diversity, where low harvest diversity is characterized by low harvest richness and evenness (i.e., single/few species dominate total harvest). (*C*) communities exhibit gradient in habitat coupling, where pie charts represent proportion of harvest obtained from each habitat. Low coupling is driven by harvest obtained predominantly from a single habitat. (*D*) harvest stability measured as the robustness of total harvest to species loss (*i*) and temporal variability in total harvest (*ii*).

Harvest Structure Metrics. Harvest diversity is the diversity of species harvested by a community, which is comparable to resource or diet diversity of consumers within food webs. Harvest diversity is a function of both the number of food species harvested (harvest richness), and evenness of harvest (i.e., Pielou's evenness). Harvest evenness is high if all species are harvested relatively equally, and low if only a few species dominate total harvest. We calculate harvest diversity as Shannon-Weiner diversity (*Materials and Methods*), which incorporates both harvest richness and evenness (Fig. 2*B*). In food web ecology, consumers that feed on a broad diversity of prey (e.g., generalists) tend to have more stable (less variable) food intake, as they are better able to switch their foraging behavior through time as different prey resources become more or less available (51). This changing prey availability is a result of variation in species responses to shifting environmental conditions that generate differential or asynchronous cycles of prey biomass over time (52). Consumers that can average over these asynchronous prey dynamics have reduced variability in total food intake (52, 53). Additionally, such adaptive foraging behavior also helps to buffer diets to the loss of any given species, increasing dietary robustness (54, 55). Ecologists define this phenomenon as a portfolio effect (36), adapted from portfolio effects in economics where diversified financial portfolios stabilize economic returns. Here, we can consider such species-level portfolio effects a mechanism through which harvest diversity increases the temporal stability and robustness of wild food harvest.

Habitat coupling describes the proportion of total food harvest derived from different habitats across heterogenous landscapes. This metric is directly analogous to habitat coupling in food webs, which is commonly used to describe the proportion of a consumer's diet obtained from two or more different habitats (51, 56, 57), such as terrestrial versus aquatic habitats. Within our framework, human communities that harvest similar proportions of food from different habitats would be considered to demonstrate a high degree of habitat coupling (see *Materials and Methods* for detailed description of metric calculation; Fig. 2*C*). In food web ecology, habitat coupling can contribute to the stability of consumer food intake through time. Different habitats often have asynchronies in the timing of when resources are available (e.g., due to differences in seasonal phenologies), and consumers that can forage across or "couple" these different habitats maintain higher and more consistent food intake over time (i.e., spatially explicit portfolio effects) (52, 58). Additionally, habitat coupling can increase the ability of consumers to buffer food intake if resources in one habitat become inaccessible or unproductive (52). As such, habitat coupling generates spatially explicit portfolio effects that, consistent with species-level portfolio effects described above, can enhance harvest stability.

Effects of Harvest Structure On Harvest Stability. As in food webs, we hypothesize that both harvest diversity and habitat coupling have the potential to influence harvest stability (Fig. 2*D*). We focus on two aspects of harvest stability: temporal harvest stability and harvest robustness. Temporal harvest stability is a measure of total harvest variability over time, measured as the coefficient of variation of harvest magnitude (biomass) through time (CV; SD/mean). CV is a common stability metric in ecology, where high CV indicates high population variability and therefore low stability, as a result of significant declines or large fluctuations in species biomass (59). In our framework, high variability in total harvest over time (i.e., low harvest consistency) indicates low temporal harvest stability. Harvest robustness is defined as the capacity for a community's total harvest to withstand the loss or significant decline of different wild food resources. This metric is analogous to robustness measures in food web ecology, which describe the magnitude of change in a system resulting from the loss of individual species (60), often measured as the number of secondary extinctions (54, 61). Here, we estimate robustness as the rate of harvest decline following simulated losses of food resources, where high rates of decline equate to rapid losses in total harvest (high magnitude of effect), indicating low robustness to species loss.

We hypothesize that harvest structure influences temporal harvest stability and harvest robustness through species-level and spatial portfolio effects. First, we predict that greater harvest diversity and habitat coupling will increase temporal harvest stability (lower CV (Fig. 2*D*) by allowing humans to harness asynchronies in the timing of when different species are available across different habitats. Second, we predict that increased harvest diversity and greater habitat coupling will increase harvest robustness in the face of species losses or declines, such that the effect of losing any given species on total harvest is reduced (Fig. 2*D*). Following this framework, we quantify wild harvest structure (harvest diversity and habitat coupling) across 46 communities in southern coastal Alaska and examine the relationship between these structural metrics and our two metrics of harvest stability (temporal harvest stability and harvest robustness).

Results

We analyzed comprehensive wild harvest data, often resolved to species-level, across 46 rural communities in southern coastal Alaska (from 1983 to 2014; *SI Appendix*, Fig. S1), where wild foods are critical to people's cultural, spiritual, economic, and nutritional ways of life [e.g., wild harvest is equivalent to ~25% of caloric and 100% of protein requirements for rural communities in the region (17)]. Communities harvested a diversity of foods across terrestrial, freshwater (including anadromous fish species), intertidal, and marine habitats. The most harvested foods, as measured by usable weight, were Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), Pacific halibut (*Hippoglossus stenolepis*), coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*), and sockeye salmon (*Oncorhynchus nerka*). Communities harvested 96 unique taxa, although the total number of species harvested is likely much greater as some species were aggregated into broader taxonomic groups in community harvest surveys (e.g., berries, plants/greens, ducks, mussels). In what follows, we characterize harvest structure for each community and demonstrate how harvest diversity and habitat coupling increase harvest stability.

Harvest Structure. We characterized harvest structure by calculating harvest diversity (HD) and habitat coupling (HC) (see *Materials and Methods* for details). Across the 46 communities, there was large variation in both harvest diversity (HD_{low} = 1.988, HD_{high} = 3.024; *SI Appendix*, Table S1) and habitat coupling (HC_{low} = 0.202, HC_{high} = 0.915; *SI Appendix*, Table S1). The range in harvest diversity and habitat coupling across all communities can be seen in simplified harvest structure representations from two communities at the endpoints of these gradients (Fig. 3). The community in Fig. 3*A* has low harvest diversity (38 taxa and HD = 2.041, where 8 taxa make up 90% of harvest) and low habitat coupling (e.g., 85% of harvest comes from freshwater/anadromous species, HC = 0.202). In contrast, the community in Fig. 3*B* has high harvest diversity (55 taxa and HD = 3.024, where 19 taxa make up 90% of harvest) and high habitat coupling (e.g., harvest is relatively evenly distributed across all four habitats, HC = 0.831). Harvest distributions for all communities can be found in *SI Appendix*, Fig. S2.

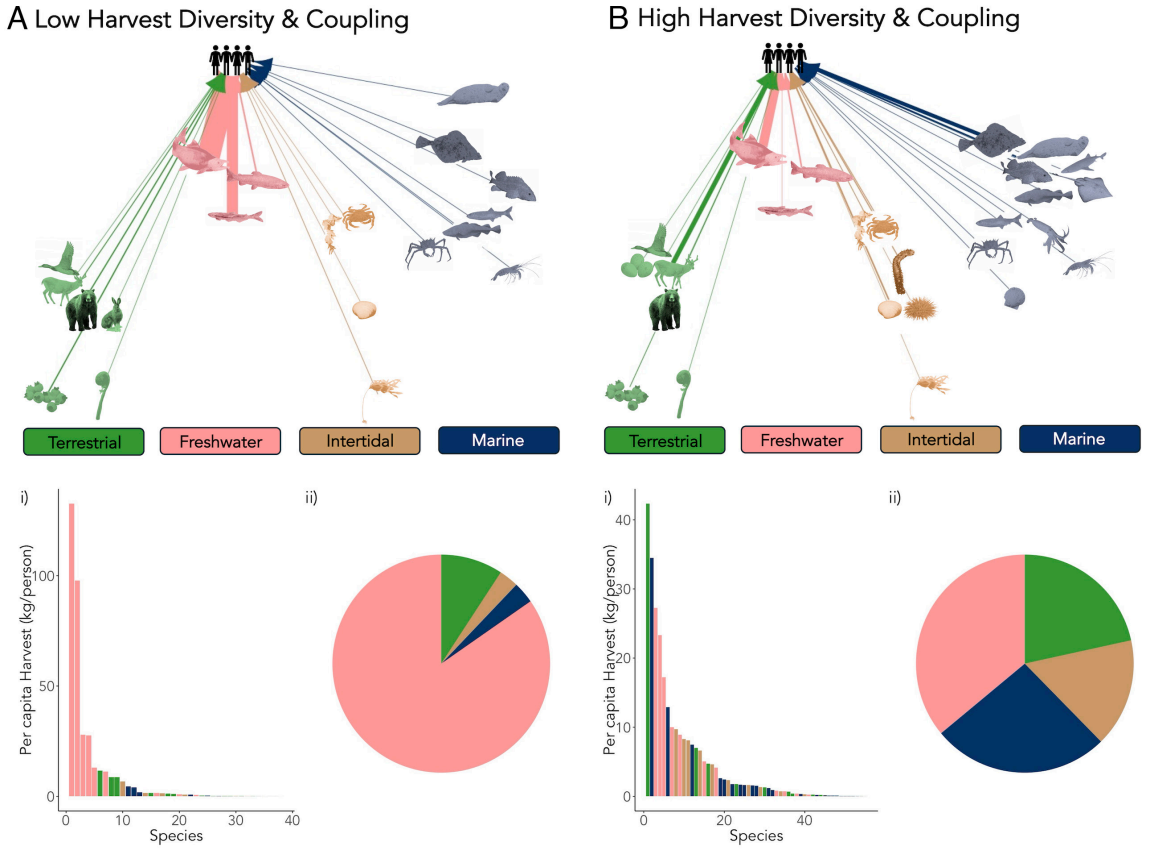

Fig. 3. Harvest structure of two example communities based on average harvest composition. (*A*) Simplified harvest structure for a community with lower harvest diversity (*i*) and lower habitat coupling (*ii*). (*B*) Simplified harvest structure for a community with higher harvest diversity (*i*) and higher habitat coupling (*ii*). The width of the lines in the harvest structures indicate annual per capita (kg/person) harvest that is obtained from each resource. Note, in some cases individual resources represent numerous species (e.g., all salmon are grouped together in these simplified structures).

Temporal Harvest Stability. We examined the influence of harvest structure on the temporal stability of total harvest by comparing harvest diversity and habitat coupling to seasonal and interannual harvest variability (CV). We estimated seasonal harvest variability by calculating intra-annual wild food harvest CV for each community (n = 46) based on taxon-specific seasonal harvest phenologies (*Materials and Methods*). We estimated interannual harvest variability by calculating CV of total harvest across years for communities where sufficient temporal surveys existed (n = 15 communities). Temporal variability in total harvest varied across communities, where larger CV values indicate higher variability in total harvest biomass. The two communities in Fig. 4 are endpoints of the gradients in seasonal and interannual harvest variability. The community in Fig. 4*A* demonstrates both high seasonal and interannual total harvest variability ($CV_{seasonal}$ = 1.531; $CV_{interannual}$ = 0.547) and the community in Fig. 4*B* demonstrates relatively low seasonal and interannual total harvest variability ($CV_{seasonal}$ = 0.701; $CV_{interannual}$ = 0.119). Seasonal harvest patterns for all 46 communities, and interannual harvest patterns for 15 communities are shown in *SI Appendix*, Figs. S3 and S4, respectively.

Harvest diversity and habitat coupling significantly reduced seasonal and interannual harvest variability (Fig. 5), such that communities that harvested a greater diversity of taxa and harvested more evenly across habitats had more stable harvest across seasons and across years (Fig. 5 *A* and *B*). Seasonally, the positive influence of harvest diversity was driven by harvest evenness whereas harvest richness had no effect, suggesting higher evenness of harvest biomass across species rather than higher number of harvested species contributes to more stable seasonal harvest (*SI Appendix*, Fig. S5*A*). At interannual timescales, the significant positive effect of harvest diversity was driven by a combination of both increased richness and higher harvest evenness, as neither richness nor evenness independently significantly reduced interannual harvest variability (*SI Appendix*, Fig. S5*B*).

At both time scales, the positive effect of habitat coupling on temporal harvest stability was greater than harvest diversity (Fig. 5 *A* and *B*). This was driven by the high degree of asynchrony in harvest across habitats (Fig. 6*A*). At the seasonal timescale, harvest was generally higher in intertidal habitats in the winter and early spring, freshwater and marine habitats in the summer, and terrestrial habitats in the fall (Fig. 6*A*). As a result of these seasonal asynchronies, CV of total harvest was significantly lower than CV of harvest within each habitat (Fig. 6*A*). While interannual asynchrony in habitats was less pronounced, we still see evidence of similar results at interannual time scales (Fig. 6*B*). These findings suggest that spatial portfolio effects may strongly contribute to consistent harvest within and across years. We also found evidence of species-level portfolio effects, such that communities harvesting species that are more asynchronous have lower harvest variability (*SI Appendix*, Fig. S6). However, greater species-level asynchrony was generally attained by harvesting species across habitats (*SI Appendix*, Fig. S7), suggesting higher harvest diversity contributes to temporal harvest stability if harvest diversity tends to be distributed across habitats.

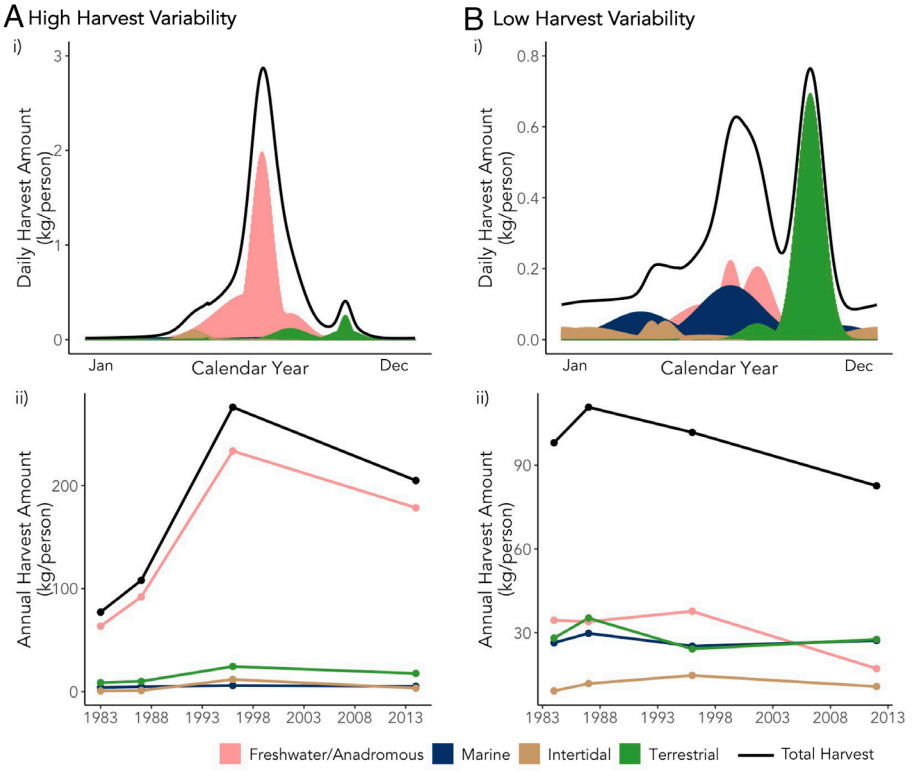

Fig. 4. Seasonal and interannual harvest patterns across habitats. Temporal harvest dynamics for two example communities exhibiting (*A*) high and (*B*) low harvest variability. (*i*) seasonal harvest distributions of each taxa across habitats and total cumulative harvest. (*ii*) interannual harvest patterns with total harvest across each habitat over time and total cumulative harvest over time.

Harvest Robustness. To estimate harvest robustness to species loss, we conducted two hypothetical knock-out experiments, a "worst-case scenario" where species were lost in order of importance to harvest, and a random-loss scenario (i.e., species randomly knocked out). We used the rate of harvest decline as a metric for harvest robustness, where rapid harvest declines with loss of single or few species were indicative of lower harvest robustness to species loss (Fig. 2*d*). We then compared the rates of harvest decline to community harvest structure.

In the worst-case scenario, harvest structure significantly influenced harvest robustness. Communities that harvested a higher diversity of foods and exhibited greater habitat coupling had significantly lower rates of harvest decline, indicating increased robustness to species loss (Fig. 5*C*). The effect of harvest diversity was driven by both harvest richness and harvest evenness, where communities that harvested a greater number of species and harvested more evenly across species had slower rates of decline (*SI Appendix*, Fig. S5*C*). For the random-loss scenario, higher harvest diversity also significantly reduced the rate of harvest decline (i.e., less negative slope, *SI Appendix*, Fig. S8*A*), which was driven by increasing harvest richness (*SI Appendix*, Fig. S8*C*), whereas evenness had no effect (*SI Appendix*, Fig. S8*D*). Additionally, in the random-loss scenario, habitat coupling had no effect on harvest robustness (i.e., no significant change in rate of decline; *SI Appendix*, Fig. S8*B*).

Within both scenarios, the positive effect of harvest diversity on harvest robustness was greater than habitat coupling (Fig. 5*C*). These results suggest that while both structural aspects of harvest patterns contribute to harvest robustness, harvest diversity may be more effective at buffering harvest against the loss of food resources. We note that our experiments assume no switching in harvest, therefore likely overestimate rates of harvest decline.

Discussion

We developed an ecological framework to understand structure–stability relationships in wild food systems. Our findings clearly demonstrate the stabilizing influence of harvest diversity and habitat coupling —harvesting more foods across multiple habitats promotes more stable provisioning of wild foods to rural communities in southern coastal Alaska. However, stability was influenced in complementary ways by different aspects of harvest structure. Wild food diversity had the strongest effect on harvest robustness. Communities that harvest more evenly across many species were more robust to the decline or loss of harvest resources. Habitat coupling, on the other hand, strongly stabilized harvest at both seasonal and interannual scales due to spatial portfolio effects that emerge from strong asynchronies in the seasonal phenology of harvest across different habitats. Our results highlight how structure–stability relationships, known to be important in food web and community ecology (48, 50, 51), can provide important insights into the stability of wild food systems.

More broadly, the ecological framework developed here provides a foundation for assessing the stability and resilience of wild food systems wherever suitable harvest data exist or can be collected. In this study, our framework's application was enabled by a distinctive dataset containing community-level harvest biomass estimates across the broad portfolio of wild foods harvested from multiple habitats. Such integrative data are uncommon, as existing datasets often focus on single habitats or taxa (e.g., fish, plants) and often lack biomass estimates. Future efforts should therefore document both the quantity and identity of species harvested across habitats and through time. Survey approaches similar to those used by the ADF&G Division of Subsistence provide a valuable model for such efforts (62, 63). Nevertheless, even where

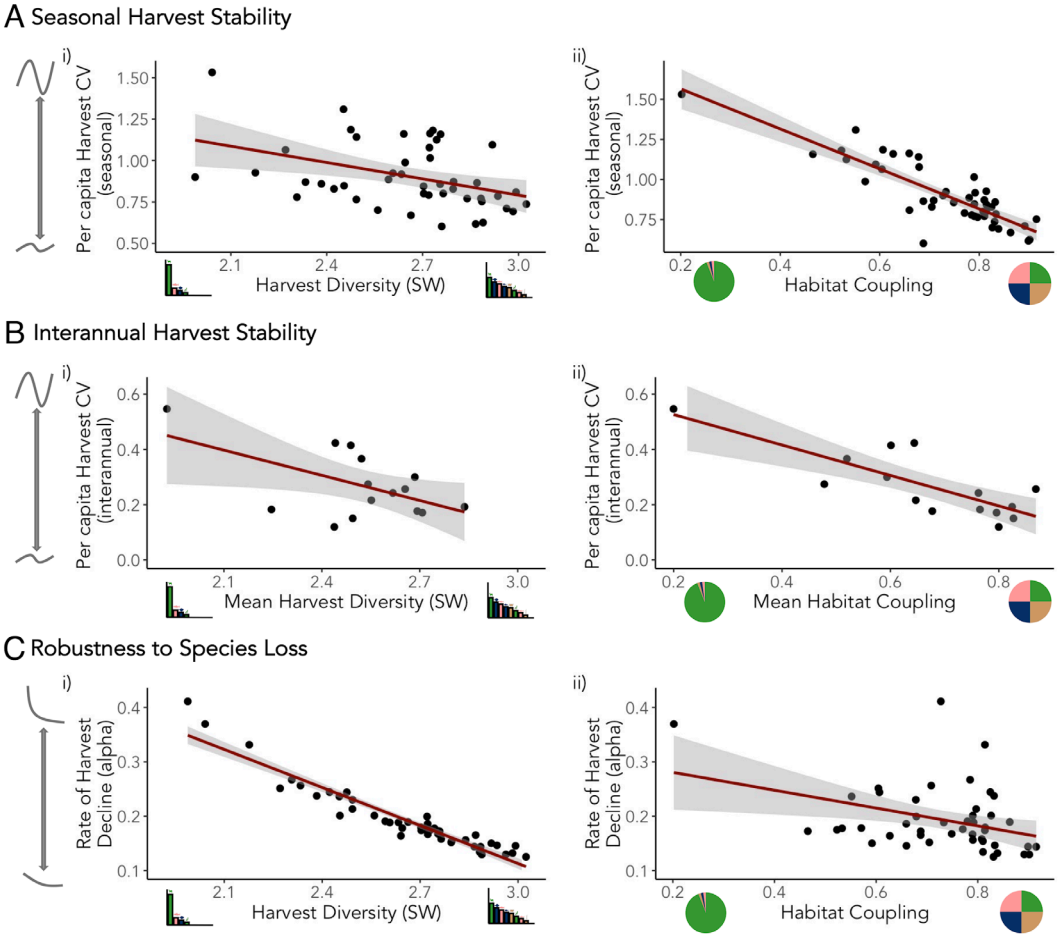

Fig. 5. Harvest structure–stability relationships. (*A*) relationship between seasonal harvest stability (seasonal total per capita harvest CV) and (*i*) harvest diversity ($F_{1,44}$ = 8.83, R^2 = 0.1482, *P* =0.0048) and (*ii*) habitat coupling ($F_{1,44}$ = 121.3, R^2 = 0.728, *P* < 0.001). (*B*) relationship between interannual harvest stability (interannual total per capita harvest CV) and (*i*) harvest diversity ($F_{1,13}$ = 5.589, R^2 = 0.2469, *P* = 0.0343) and (*ii*) habitat coupling ($F_{1,13}$ = 23.23, R^2 = 0.613, *P* <0.001). (*C*) relationship between robustness to species loss (rate of harvest decline) and (*i*) harvest diversity ($F_{1,44}$ = 426.2, R^2 = 0.904, *P* <0.001) and (*ii*) habitat coupling ($F_{1,44}$ = 6.97, R^2 = 0.117, *P* = 0.011). Icons on x and y-axes display schematic representations of high and low values presented here, the context of which are explained in Fig. 2.

data are limited to specific taxa or habitats, components of our framework can be applied. For instance, robustness and temporal variability in fish harvest can be linked to harvest diversity and habitat coupling (e.g., the relative contribution of offshore vs. nearshore species) by integrating existing harvest records with species life-history information and harvest timing from literature and local knowledge. Incorporating local and Indigenous knowledge remains essential to accurately represent these systems and their dynamics, as their extensive knowledge is often not captured in published literature (64).

Rural communities in southern coastal Alaska harvest a diversity of resources as a way of life and a strategy to navigate environmental variation and uncertainty (28–30, 65). Harvest diversity can help overcome fluctuations in resource abundance by providing dietary redundancies, which can help maintain sufficient caloric and nutritional intake, and enhance communities' adaptive capacity and resilience (28, 66). This behavioral harvesting strategy is analogous to generalist consumers within ecosystems, where species that forage on a diversity of resources tend to be better adapted to variable environments (67, 68). Diet diversification helps to "buffer" consumers against the loss or decline of a given set of resources, and theory has shown that the ability to rapidly respond to changing resource conditions strongly stabilizes consumer populations to whole ecosystems (51, 53, 69). Our results extend these ecological ideas to human communities—harvesting a diversity of species buffers communities to shifting resource availability over time, as we demonstrate via significant positive effects of harvest diversity on both harvest robustness and temporal harvest stability at seasonal and interannual time scales. Our findings also highlight the potential stabilizing influence of harvest evenness. While not explicitly explored here, increased harvest evenness may make harvest compensation more achievable, for example, if the harvest of salmon and deer are relatively even, less effort and time may be required to compensate for a decline in the availability of either species.

We illustrate that communities access wild foods across multiple different habitats and ecosystems to diversify food resources and capitalize on asynchronous seasonal resource pulses (30, 35, 70). These seasonal patterns of harvest are strongly rooted in Indigenous knowledge systems [e.g., seasonal round, harvest calendars (34, 37, 44)] and highlight how traditional ways of life have developed robust harvest strategies and behavioral adaptations to maintain harvest in variable environments. Ecologists have described similar behaviors in mobile generalist species that harness spatiotemporal portfolio effects by coupling habitats in space and time to access consistent resource supplies in variable environments (51, 53, 56). Our framework applies these ideas of spatiotemporal habitat coupling to describe human harvest patterns and demonstrates how increasing coupling across habitats significantly stabilizes wild food harvest over time. Importantly, the reduction in total harvest CV

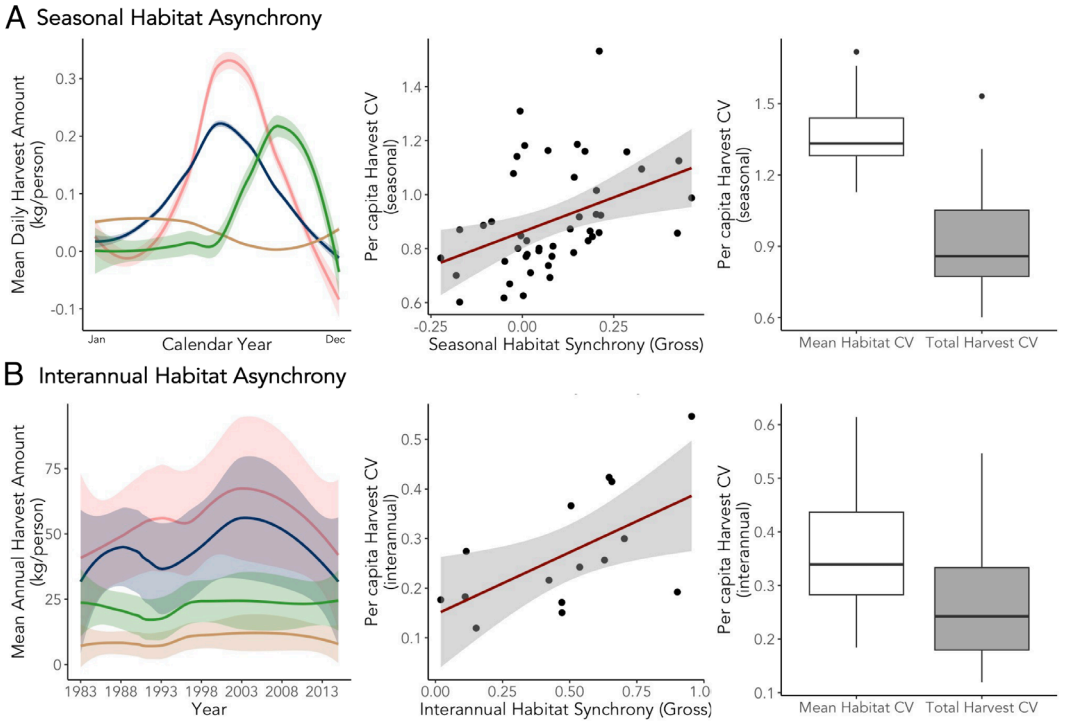

Fig. 6. Habitat asynchrony and spatial portfolio effects at (*A*) seasonal and (*B*) interannual time scales. (*Left* column) Mean harvested biomass across habitats. Lines generated from smoothed locally estimated scatterplot smoothing (LOESS) function across daily or annual means from each community; the shaded area represents 95% CI. (*Middle* column) Influence of asynchrony in harvest timing across habitats (Gross synchrony metric) on total per capita harvest CV (seasonal: $F_{1,44} = 8.554$, $R^2 = 0.144$, $P = 0.005$; interannual: $F_{1,13} = 6.945$, $R^2 = 0.298$, $P = 0.021$). (*Right* column) Boxplot of CV across communities for average habitat CV (i.e., mean CV for each habitat within a community) and total harvest CV (seasonal: $H_1 = 59.284$, $P < 0.001$; interannual: $F_1 = 5.492$, $P = 0.0191$).

relative to within-habitat CV suggests that communities harness spatial portfolio effects generated by the strong seasonal asynchrony in harvest availability between different habitats. Such insights highlight the importance of promoting access to wild food sources across diverse landscapes to help communities adapt to shifting environmental conditions (71).

Collectively, our results suggest that wild food diversity and access to wild foods across multiple different habitats are important for maintaining robust and consistent harvest levels over time. These findings provide important insights into managing landscapes to maintain stable and resilient wild food systems as climate change, land use, and other factors influence the availability and accessibility of wild foods. From an ecological perspective, these findings emphasize the importance of management strategies and regulations that maintain (or improve) the capacity and flexibility for communities to access diverse harvest resources across heterogenous landscapes (30). In southern coastal Alaska, the regulatory environment challenges this flexibility as different habitats and different food sources are managed by different organizations across federal and state agencies (33). Continued frequent evaluations of harvestable amounts and harvest seasons and reciprocal communications between harvesters and regulators [e.g., through Regional Advisory Councils (72)] are necessary to provide adaptable, flexible, and sustainable harvest strategies.

Furthermore, working with local communities and weaving together local/Indigenous knowledge with Western scientific approaches may improve management and support continued access to managed landscapes. Communities harvesting wild foods have a deep understanding of historic and on-going environmental changes that may not be captured with existing monitoring programs (37). For instance, rural communities in southern coastal Alaska have developed sustainable harvest practices that promote wild food harvest from multiple habitats, which reduces the risks posed by species decline and environmental change. Management strategies that respect and integrate local/Indigenous governance systems and flexible harvest policies are essential for maintaining both harvest stability and structure in the face of shifting environmental conditions. Such approaches can also help sustain access to landscapes that are integral to the ways of life of local and Indigenous communities, and are essential for fostering resilient and just food futures (73). Future research that engages Tribal members and other harvesters could improve understanding of species responses to environmental change and inform equitable management strategies adapted to local conditions. We also acknowledge that wild food systems are a function of ever changing social, economic, and political systems (4, 28). Indeed, the harvest structures reported in our study are the outcome of these intertwined drivers and changes to these factors should be considered when assessing future resilience of wild food systems.

As the world grapples with developing sustainable food production systems that provide sufficient food for the growing global population, integrating wild foods into sustainable food system development can help diversify food production sources that promote food security and ecosystem services. We illustrate that ecological mechanisms that stabilize ecosystems may also underpin the stability of human wild food systems. Our findings emphasize the importance of maintaining heterogeneous landscapes that support a diverse portfolio of wild food species, as well as flexible regulations that allow harvesters to adapt to changing patterns of food availability. Importantly, such management approaches can also help support food production landscapes that maintain biodiversity and landscape heterogeneity, which researchers have identified as key aspects needed to sustain the productivity and stability of both food systems and ecosystems (6).

Materials and Methods

Study Area. We analyzed wild foods harvest data from 46 rural communities across southern coastal Alaska (SCAK). SCAK includes the coastal regions of southeast and southcentral Alaska, which are home to the Tongass and Chugach National Forests, the two largest National Forests in the United States that together comprise over 9 million hectares (*SI Appendix*, Fig. S1). These National Forests represent the northernmost extent of the largest intact temperate rainforest in the world, with diverse landscapes encompassing alpine zones, mid- and low-elevation forests, wetlands, glaciers, lakes and rivers, intertidal zones, and nearshore marine ecosystems.

The 46 rural communities in this coastal region rely on these landscapes for wild harvest (*SI Appendix*, Fig. S1), which can contribute an equivalent of ~17% of caloric and 100% of protein requirements for some communities (17). These communities are small and remote; population size between 1980–2020 varied from 32 to 8,513 people (74) most communities are off the road system and only accessible by boat or plane, with an average distance of 122 (±63.61) km to the nearest urban city (i.e., Juneau, Anchorage, or Ketchikan, the designated urban cities during survey periods).

Harvest Data. To help inform wild harvest (also termed subsistence) regulations, the Alaska Department of Fish and Game (ADF&G) Division of Subsistence conducts periodic household surveys in communities to document harvest of wild foods (i.e., all finfish, shellfish, wildlife, and wild vegetation) and generate comparable, quantified data at a household level. The surveys document all harvests for home use during the study period, including wild resources taken under federal subsistence, state subsistence, personal use, general, and sport regulations, as well as fish removed from commercial harvests for personal use. Community-level subsistence harvest data for each community and study year are housed in the online Community Subsistence Information System (https://www.adfg.alaska.gov/sb/CSIS/). Detailed information on survey methods and community harvest estimates can be found in the whitepaper ADF&G, 2019 (63), and the division's technical paper series (http://www.adfg.alaska.gov/sf/publications/).

We extracted estimated per capita (kg/person) harvest data for all taxa included in the comprehensive surveys from all available years for the 46 communities. Surveys occurred between 1983–2014 and the number of surveys per community varied from 1 to 9, where 15 communities had 3 or more surveys spanning at least 12 y. The taxonomic resolution of some food sources in the surveys increased over time (e.g., from ducks to specific species of ducks), therefore we identified the lowest common taxonomic level across all surveys and summed per capita harvest to generate comparable surveys across all communities and time points. We then assigned each taxon to a given habitat (i.e., terrestrial, freshwater (including anadromous fish), nearshore intertidal, and marine) based on that species' life history information.

Last, we developed taxon specific seasonal harvest phenologies to examine seasonal harvest dynamics. First, we identified taxa that on average collectively comprised 99% of the total harvest of all taxa across the 46 communities. Then, for each of these taxa we used existing Western scientific and local knowledge from multiple source types (e.g., hunting and fishing regulations, ADF&G general fish availability, peer-reviewed literature, white papers, field guides, books, personal communications) to generate a best estimate of harvest start dates, end dates, and peak harvest dates (see *SI Appendix*, Table S2 for list of sources and harvest window dates). We then developed either unimodal or bimodal normal distributions with mean of peak harvest date(s) and SD of 0.1*length of harvest window (i.e., number of days) for each taxon. Then, for each community's harvest composition (average and annual; see below), we distributed the per capita harvest of each taxon across the given harvest window. We note that we make two simplifying assumptions: First, we considered harvest windows static across space and time, and second, we assumed that harvest was normally distributed across the harvest window. This provides important opportunities for future work to explore different distributions and dynamic harvest windows, yet this is beyond the scope of this paper.

Characterizing Harvest Structure. To examine differences in harvest structure across communities and over time, we generated two types of harvest compositions: average harvest composition and annual harvest composition. Average harvest compositions were determined by calculating the average per capita harvest of each comparable taxonomic level from all surveys over time for each community. Annual harvest compositions were generated for each survey year for the 15 communities with more than 3 surveys using per capita harvest at the lowest common taxonomic resolution. We then visualized each harvest structure for each community or year using network graphing approaches. For presentation, we simplified harvest structures to display major resource groups (e.g., salmon, large land mammals, etc.) and used the network plotting R package *igraph*, where each "edge" (i.e., interaction between community and harvest resource group) was weighted by per capita harvest (for aesthetic purposes, edges in Fig. 3 are 1/5 of per capita harvest). Images of harvested resources were generated by Cecil Howell.

For each harvest composition we characterized harvest structure by calculating harvest diversity (and its components: harvest richness and harvest evenness) and habitat coupling. We calculated harvest diversity as Shannon-Weiner diversity index using the *vegan* package (75) in R, where per capita harvest biomass was used as an indicator of relative abundance. We then partitioned the SW diversity into metrics of both richness (number of resources harvested) and Peilou's evenness index [SW diversity/log(richness)]. We then constructed a metric to calculate habitat coupling (i.e., evenness in the proportion of total harvest derived from different habitats) across 4 habitats (terrestrial, freshwater/anadromous, nearshore intertidal, and marine) for each communities' harvest composition. We first calculated the proportion of harvest from each habitat and then, to estimate relative evenness of harvest across these habitats, we calculated the SD of harvest proportions between the four habitat types. Communities that harvest evenly across habitats (i.e., 25% of their total harvest from each of 4 designated habitats) would be considered to have the highest degree of habitat coupling and would also have a SD of 0 (i.e., proportion of harvest perfectly even). A high SD would indicate low habitat coupling (i.e., a single habitat dominates harvest). For simplicity, we normalized SD to create a simple habitat coupling (hc) metric between 0 to 1, as follows:

$$hc = 1 - \left(\frac{SD}{0.50}\right),$$

where a community with hc = 0 exhibits no coupling (i.e., 100% of the harvest comes from 1 habitat) and a community with hc = 1 exhibits maximum coupling (i.e., exactly 25% of harvest comes from each habitat). For any further statistical analysis, values were logit transformed to improve normality.

Assessing Harvest Stability. We analyzed two types of harvest stability that have important implications for food security. The first is temporal stability, which we define as the variability (coefficient of variation, CV) in total harvest biomass over time. CV is a common metric used in ecological research to quantify the temporal stability of a given population or community (59).The second is the robustness to species loss, which we define as the capacity for a community's total harvest to withstand the loss or significant decline of different wild food resources.

Temporal stability. We calculated the coefficient of variation (CV) of total harvest (i.e., sum of all individual species harvested) at two temporal scales: seasonal and interannual. To quantify seasonal harvest stability, we calculated the CV of daily total per capita harvest of all resources based on the seasonal harvest phenology of each taxon. To quantify interannual harvest stability, we calculated the CV of total annual harvest over time (i.e., between sampling years). Seasonal and interannual total harvest dynamics and associated CV for all communities are shown in *SI Appendix*, Fig. S9.

Robustness to species loss experiment. To quantify robustness, we conducted a series of hypothetical knock-out experiments that remove harvest resources and calculate the subsequent magnitude of change in total harvest. These knock-out experiments consisted of two scenarios: 1) The "worst-case scenario" where the loss of species followed the order of importance, such that the most harvested species are lost first; and 2) The "random scenario" where species losses occur randomly. For the worst-case scenario, we calculated nonlinear exponential decay functions for each community and used the exponent alpha, which describes the rate of total harvest decline as the robustness metric. High rates indicate harvest is strongly affected by the loss of a few species (and thus a less robust harvest) and lower rates of decline indicate harvests that are more robust to the loss of species. For the random knock-out scenario, we iterated random species loss 855 times and then calculated linear regressions for each scenario. We extracted the slopes from each iteration as the robustness metric (analogous to rate of decline) and calculated mean and SD of slopes for each community. Within these

experiments we assume that communities do not exhibit any switching behavior (i.e., compensating for loss or reduction of a given species), thus the rates of decline likely overestimate the actual rate of decline in total harvest a community would experience. The two different model forms (i.e., nonlinear exponential decay and linear regressions) were used to provide best fit rate of declines for the given scenario. Results from each scenario for all communities are shown in *SI Appendix*, Fig. S9.

Assessing Harvest Structure Influences on Harvest Stability. To assess the influence of harvest structure on harvest stability we conducted simple linear regressions between each structural metric (i.e., harvest diversity and habitat coupling) and each stability metric (i.e., seasonal CV, interannual CV, robustness). To parse out the role of richness vs. evenness of harvest in the observed harvest diversity–stability relationships, we conducted linear regressions between each component and each stability metric.

To elucidate potential mechanisms that contribute to differences in temporal harvest stability and if communities harness asynchronies in resource availability across species and habitats, we calculated harvest synchrony across habitats and across species at both the seasonal and interannual scales. We calculated temporal synchrony of per capita harvest between the four habitat types using the Gross synchrony metric (76) that calculates synchrony as the average of the correlation between the biomass of harvest in each habitat and the total harvest across all other habitats. The metric scales from −1 to 1, where −1 indicates harvest across habitats are maximally asynchronous, and +1 indicates harvest is perfectly synchronous. We also calculated Loreau synchrony metrics (77) and found consistent results (*SI Appendix*, Fig. S10). We then conducted linear regressions between synchrony and seasonal and interannual CV, for both species–level and habitat synchrony,

Last, to test for presence of species–level and spatial portfolio effects, we calculated and compared the mean CV of harvest from each habitat or the mean CV of harvest from each species and the mean CV of total harvest at seasonal and interannual scales. The reduction in CV at aggregate scales (i.e., total harvest) are indicative of humans harnessing differential or asynchronous harvest availability between habitats or species. We checked ANOVA assumptions using Levene's test for homogeneity of variance and Shapiro–Wilk test for normality. Both seasonal and interannual data satisfied homogeneity of variance assumption (seasonal: $F_{1,90} = 3.365$, $P = 0.07$; interannual: $F_{1,28} = 0.142$, $P = 0.71$), however failed the normality test (seasonal: $W = 0.952$, $P = 0.002$; interannual: $W = 0.927$, $P = 0.041$). Therefore, we conducted a nonparametric Kruskal–Wallis test to detect significant differences in habitat CV and total harvest CV.

All analysis was conducted in R v. 4.3.2 (78). All data and code used to generate results are available at the following GitHub repository: https://github.com/mariegutgesell/wild_foods_repo (79).

Data, Materials, and Software Availability. csv, R code data have been deposited in wild_foods_repo (https://github.com/mariegutgesell/wild_foods_repo).

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