



# Benefits and risks of diversification for individual fishers

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**Individuals relying on natural resource extraction for their livelihood face high income variability driven by a mix of environmental, biological, management, and economic factors. Key to managing these industries is identifying how regulatory actions and individual behavior affect income variability, financial risk, and, by extension, the economic stability and the sustainable use of natural resources. In commercial fisheries, communities and vessels fishing a greater diversity of species have less revenue variability than those fishing fewer species. However, it is unclear whether these benefits extend to the actions of individual fishers and how year-to-year changes in diversification affect revenue and revenue variability. Here, we evaluate two axes by which fishers in Alaska can diversify fishing activities. We show that, despite increasing specialization over the last 30 years, fishing a set of permits with higher species diversity reduces individual revenue variability, and fishing an additional permit is associated with higher revenue and lower variability. However, increasing species diversity within the constraints of existing permits has a fishery-dependent effect on revenue and is usually (87% probability) associated with increased revenue uncertainty the following year. Our results demonstrate that the most effective option for individuals to decrease revenue variability is to participate in additional or more diverse fisheries. However, this option is expensive, often limited by regulations such as catch share programs, and consequently unavailable to many individuals. With increasing climatic variability, it will be particularly important that individuals relying on natural resources for their livelihood have effective strategies to reduce financial risk.**

diversity-stability relationship | Bayesian variance function regression | income variability | natural resource management | ecological portfolio effects

It can be difficult for individuals to sustain a livelihood from natural resource extraction. These livelihoods tend to have high annual variability in income relative to other professions (1, 2). In addition to income variability from economic sources, such as changes in demand or prices, individuals dependent on natural resources are also subject to biological and environmental variability (3). For example, drought and flooding are a major source of risk for agricultural food security and farmers' incomes (4), and catastrophic disease outbreaks and wildfires increase risk for the logging industry (5).

Individuals who rely on natural resources for income develop strategies to reduce income variability. For example, farmers may diversify their crops or include off-farm income sources to buffer against environmental and market shocks, as well as long-term climatic trends and seasonality (6–8). However, otherwise well-intentioned regulations may limit how individuals diversify, or may incentivize against diversification. For instance, crop subsidies in the United States may incentivize some farms to special-

ize [e.g., dairy, grains, soybeans (1)]. In other instances, market forces (e.g., prices or demand) may discourage the adoption of diverse strategies and help promote specialization (9).

Diversification may benefit commercial fishers, given the extreme economic risk that some individuals experience, particularly relative to terrestrial agriculture (2). The majority of risk insurance programs available to terrestrial farmers (e.g., crop insurance programs) are not available to commercial fishers (10). However, fishers may be able to lower risk by diversifying their fishing portfolio. They can, for example, target as many species as allowed by a permit, own multiple permits, or diversify spatially and fish in multiple regions. The effectiveness of these diversification strategies for increasing revenue and reducing revenue variability remains uncertain. Theory and empirical studies demonstrate that there can be substantial benefits to specialization for both farmers and fishers (3, 11, 12). Furthermore,

## Significance

**Individuals who rely on natural resources for their livelihoods, such as fishers, farmers, and forestry workers, face high levels of income variability. For fishers, catching multiple species has been shown to reduce revenue variability at large scales (vessels and communities), but the individual-level consequences of maintaining catch diversity are unknown. Our work demonstrates that individuals in fisheries targeting a diversity of species and individuals who participate in multiple fisheries buffer income variability compared with less diverse individuals. However, large adjustments in diversification strategies from year to year are risky and usually increase revenue variability. The most effective option to reduce revenue variability via diversification—purchasing additional permits—is also expensive, often limited by regulations, and therefore unavailable to many.**

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Data deposition: The fisheries data that support the findings of this study, although confidential, are available from the Commercial Fisheries Entry Commission (<https://www.cfec.state.ak.us/>), and summaries used in this paper, along with all code, are archived at GitHub (<https://github.com/NCEAS/ptfx-commercial>) and Zenodo (<https://doi.org/10.5281/zenodo.883628>).

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the majority of research examining the effects of diversification on revenue does so at aggregate levels that combine individuals [e.g., counties or communities (10, 13, 14)]. Thus, key uncertainties remain about the relationship among diversity, fishing revenue, and fishing revenue variability at the level of the individual.

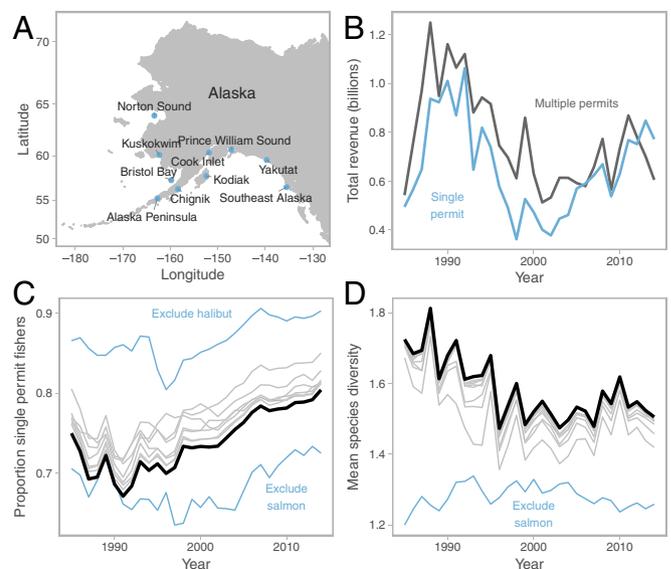
The state and federal fisheries of Alaska provide a unique opportunity to understand the role of individuals' strategies in determining income and income variability. Fisheries in Alaska are among the highest-valued fisheries in the world, with ~2.7 billion kilograms of landed biomass valued at nearly 2 billion USD annually (15). Fishers must own a permit to participate in virtually all fisheries (16). While such regulations have helped reduce overfishing and, in many fisheries, have increased profits, they limit the available strategies to reduce income variability. For example, many permits limit fishing to a single species, diversifying by purchasing additional fishing permits can be expensive, and some fisheries limit the entry of new participants through individual fishing quotas (IFQs) (17). (For example, it cost ~\$192K USD for a king and tanner crab permit in southeast Alaska in 2017: [https://www.cfec.state.ak.us/pmtvalue/X\\_K69A.HTM](https://www.cfec.state.ak.us/pmtvalue/X_K69A.HTM).)

Using a unique dataset collected over 30 y on individual fishers, rather than fleets or vessels, we examine how revenue and revenue variability of individuals is affected by diversification. By tracking individuals, it is possible to track people who switch fishery permits over time or use multiple vessels and to differentiate fishers who share the same vessel. To simultaneously understand the effect of species diversity within fisheries catches on individual revenue and revenue variability, we develop a hierarchical variance function regression model (18, 19). Our model builds on results from vessel (10), fleet (2), and community-level (13, 14) variability, and, although we model revenue variability, we herein equate revenue variability with financial risk for consistency with Kasperski and Holland (10). [More specifically, variability is one component of risk. Risk combines elements of variability, uncertainty, and loss to define the "possibility of a bad thing happening" (20).] We simultaneously estimate the effect of species diversity [the inverse of Simpson's concentration index (21, 22)] on individual revenue and revenue variability, and estimate effects both within and across fishing strategies while controlling for fishing effort and latent time effects (e.g., changing environmental conditions). We use the model to evaluate two axes by which fishers in Alaska can diversify fishing activities: (i) choice of permit strategy (i.e., permit or set of permits fished) and (ii) choice of what species to fish within a permit strategy.

## Results

We evaluated trends in revenue and diversification over time for individuals fishing commercially in Alaska from 1985 to 2014 (Fig. 1A). The majority (70 to 90%) hold a single permit, with a slight increase in single-permit holders since 2000 (Fig. 1C). This overall trend is most sensitive to halibut or salmon permit holders: Compared with other fisheries, halibut permit holders are more likely to hold halibut plus other permits, whereas salmon permit holders are more likely to hold a single permit (Fig. 1C). Despite making up only 10 to 30% of the individuals, multiple-permit holders earn approximately half the overall revenue (Fig. 1B). The mean species diversity of the catch that generated this revenue declined somewhat from 1985 to 2000 but has since remained steady (Fig. 1D). This trend appears largely driven by an increase in salmon specialists in the late 1980s and the 1990s, and it disappears if salmon license holders are excluded (Fig. 1D).

Individual revenue variability decreases exponentially with higher mean fished species diversity across combinations of state and federal fishing permits ("strategies"; Fig. 2). This pattern is



**Fig. 1.** Trends in revenue and diversification over time. (A) Map of major fishing areas in Alaska. (B) Total revenue in billions of USD from 1986 to 2014 for multiple-permit (gray) and single-permit (blue) holders. (C) Proportion of single-permit holders for all fisheries (thick black line) and with permit holders omitted each year who fished any of the nine top species groups (thin lines). (D) Mean effective diversity of species fished (Simpson's diversity index) for all fisheries (thick black line) and with permit holders omitted each year who fished any of the nine top species groups (thin lines).

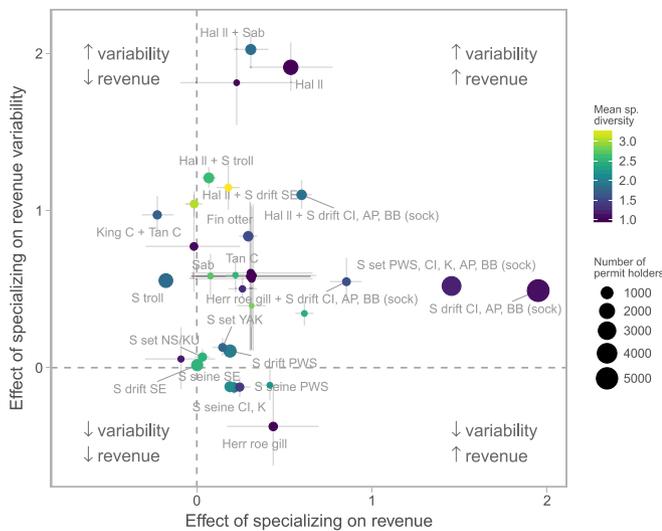
qualitatively similar with or without individuals targeting salmon. Controlling for effort, strategies with one unit higher mean species diversity had, on average, 38% (31 to 47%, with 95% CI) lower variability. As examples, revenue variability was highest for the herring roe gillnet and king crab fisheries. Most strategies with the lowest estimated revenue variability combined halibut with a salmon permit and had high levels of fished species diversity (Fig. 2).

Comparing single-permit holders to individuals holding that same permit plus additional permits illustrates the expected reduction in year-to-year revenue variability from purchasing additional permits (Fig. 3 and Fig. S1). For example, individuals fishing a halibut permit plus one additional permit always had lower expected revenue variability compared with individuals fishing only a halibut permit [median reduction of 49% (42 to 55% interquartile range), Fig. 3A]. Likewise, adding a permit to a herring roe gillnet strategy substantially reduced expected revenue variability (Fig. 3B). Adding permits also usually increased expected revenue, although the permits themselves represent a significant expense.

In contrast to the clear across-strategy effects of species diversity on revenue and revenue variability, the effect of changing fished species diversity for an individual within the constraints of a given strategy (set of permits) is more variable (Fig. 4). After accounting for fishing effort and changes in annual average revenue for fishers with the same set of permits, specializing tends to be associated with increased revenue but also increased variability (Fig. 4 and Figs. S2–S4). On average, there is a ~0.5% increase in the year-to-year revenue ratio per 1% decrease in species diversity, and, across strategies weighted equally, 93% of the probability density supports a positive relationship between specialization and revenue. However, when not controlling for effort, the average effect of specializing on revenue becomes more neutral (Fig. S5).

Changing (increasing or decreasing) an individual's fished species diversity within the constraints of a strategy tends to be associated with greater expected variability or uncertainty





**Fig. 4.** Effect of specializing on year-to-year changes in revenue and revenue variability for individual permit holders within the 34 most common strategies. Changing species diversity from year to year is associated with higher variability for individuals within the strategies above the zero line. Specializing is associated with greater expected revenue ratios to the right of the zero line and lower expected revenue ratios to the left of the zero line. For example, individuals with setnet permits for salmon in Prince William Sound, Cook Inlet, Kodiak, Bristol Bay, or the Alaska Peninsula (second purple dot from right) target primarily sockeye salmon and experience a ~1.5% increase in their year-to-year revenue ratio (horizontal axis) and a ~0.5% increase in their revenue variability (vertical axis) for a 1% decrease in their ratio of year-to-year species diversity. These effects are estimated holding fishing season length constant from year to year. Dots and line segments represent medians and 50% credible intervals, respectively, of posteriors. In other words, the axes represent coefficient values from the strategy-level slopes. Moving along an axis (say from left to right on the horizontal axis) represents an increase in how steep the slope is between specialization and the year-to-year revenue ratio. The effect of generalizing (increasing species diversity) is similar (Fig. S4). Species groups: Dun C, dungeness crab; Fin, finfish; Hal, halibut; Herr, herring; King C, king crab; S, salmon; Sab, sablefish; Sea cuc, sea cucumber; sock, sockeye salmon; Tan C, tanner crab. Gears: drift, drift gillnet; gill, gillnet for herring; Il, longline; otter, otter trawl; set, setnet. Regions: AP, Alaska Peninsula; BB, Bristol Bay; CH, Chignik; CI, Cook Inlet; K, Kodiak; KU, Kuskokwim; NS, Norton Sound; PWS, Prince William Sound; SE, Southeast Alaska; YAK, Yakutat.

long-term risks if market, management, biological, or environmental conditions change. For example, US farmers specialized on wheat, corn, or soybeans were hit harder than diversified farmers in the early 1980s when a financial crisis hit (26). Third, diversifying—a lack of specialization—can happen as a consequence of nonideal circumstances such as poor availability of a more valuable resource. For example, Ugandan households relying on forestry resources for income increase their income portfolio diversity following downward economic shocks (29). Because specialization inherently holds risk from “putting all one’s eggs in one basket,” it is not surprising that a decline in the most valuable resource would lead to a shift toward diversification. Conversely, a specialization may appear as a response to increased revenue. A fisher who achieves high revenue from a hotspot of a particular fish species one year may choose to stop or pause fishing, thereby indirectly limiting catch diversity. For example, pink and chum salmon are the dominant species caught in purse seine fisheries in Prince William Sound, with chum salmon generally harvested earlier in the season than pink salmon. If fishers targeting chum salmon achieve high revenue early in the season, they may choose to fish less later in the season.

We also found that, within strategies, altering species diversity tended to be associated with increased revenue variability.

There are a number of possible reasons for this relationship. For instance, local knowledge and experience are a major determinant of fishing efficiency (30). Therefore, changes to fishing patterns may sometimes be associated with a learning or adaptation phase as individuals become accustomed to new locations, gear, or species. Additionally, changes in diversity might reflect years in which targeted species were less available and fishers instead chose to target other species or landed more nontarget species, adding stochasticity to their revenue. Most importantly, this increased variability reflects an inability for our model to predict an individual’s revenue in a subsequent year. There are many reasons, often unique to an individual permit holder’s behavior (30–32) and therefore not in our model, that might make a specific individual’s revenue less predictable if species diversity changes.

There are many possible barriers to diversification for individuals relying on natural resources for their livelihood. A primary barrier is the cost of diversifying. For commercial fishers, purchasing additional licenses and gear typically represents a substantial expense. Related barriers are apparent in other natural resource sectors. For example, diversification has been positively linked with total income or access to financial capital for farmers (7, 33), small-scale fishing communities (34), and those relying on forest resources (35). While we were unable to incorporate costs, it is possible that including license and gear purchase costs along with others, such as costs of gear maintenance, catch transportation, and selling to a processor, would alter the relationship between catch diversification and profits. Another major barrier to diversification can be management restrictions. In commercial fisheries, regulations that have been shown to reduce overfishing—including improved assessments (36) and individual quota systems (37)—may ultimately restrict individual diversification (3, 10) or at least make developing a diverse fishing portfolio more expensive. However, individual quota systems, in particular, may also reduce income variability (Fig. S64), perhaps offsetting the effects of reduced diversification (38).

Our analysis provides a synthetic view of the effects of species diversity on individuals over 30 y in one of the most productive fishing regions in the world. Although we focus on Alaska, and expect our results are largely generalizable to other productive and intensely managed fishing regions, it is possible that the benefits of diversification would be stronger in regions where fish stocks are highly variable or in regions where permit costs are lower and more freely available. Furthermore, in addressing the overall pattern, we have averaged out the potential signal of several major discrete events, such as the *Exxon Valdez* oil spill in 1989, that was a significant disruption to the management, ecological, and social structure of fisheries in Alaska (39). In addition to revenue or income variability, it is important to understand the benefits of diversification in the context of rare and extreme disturbances which occur in natural systems worldwide (40).

With increasing environmental variability and extreme events in a changing climate (41), it is particularly important that individuals who rely on natural resources as a primary source of income, such as fishers, farmers, and forestry workers, have effective strategies to reduce risk. While diversification can provide a powerful form of risk buffering, we have shown that the relationship between individual changes to diversification and income variability is complex and context-specific. Furthermore, external market forces can interact with management regulations, which have other considerable benefits, to restrict individual diversification opportunities and promote specialization. From a management perspective, metrics such as interannual variability in individual fishing revenue or fraction of single-permit holders within communities could serve as bioeconomic indicators. Although variability in individual revenue is not yet actively incorporated into management decisions, analyses such as ours help to explain the range of diversification strategies available,

trade-offs inherent in such management decisions, and how these trade-offs may change over time.

## Materials and Methods

**Data.** We obtained commercial fisheries landings and revenue data for all target and nontarget species for permit holders in Alaska from 1985 to 2014 from the Alaskan Commercial Fisheries Entry Commission (CFEC). These data represent a total of nearly 43 billion 2009 USD. We adjusted for inflation by setting all revenues to 2009 USD (42). We implemented a number of filtering steps to focus on individuals actively engaged in commercial fishing (*Filtering Data and Grouping Permits into Strategies*). In particular, we removed permit holders whose median revenue was <\$10,000 USD, to focus on individuals with substantial income from commercial fishing.

We used combinations of state and federal fishing permits held by an individual in a specific year to define fishing strategies, representing the species caught. For example, we combined permits that were otherwise the same except for vessel size (e.g., a longliner fishing sablefish on a vessel under 60 ft was considered to have the same strategy as a longliner fishing sablefish on a vessel over 60 ft), and we combined a number of permits that were for a single species and differed only in region fished. For example, someone fishing herring roe in Kodiak and someone fishing herring roe in Alaska Peninsula were both considered to have a “herring roe” permit strategy. For salmon permits, we formed salmon strategies based on similarities in gear type and species composition (*Filtering Data and Grouping Permits into Strategies*). Gear types and permits are closely linked since, in most cases, a fisher would require a different permit to use different gear. The ability to diversify without changing or adding gear or permits is therefore driven by biological availability and choices by fishers, such as fishing early versus late in a year or fishing in particular locations.

After this process of combining permits, we were left with 23 unique fishing permit groups (Table S1), which we aggregated within each person-year combination to form permit strategies. For example, if someone fished halibut and sablefish in the same year, their strategy for that year would be “halibut-sablefish.” Specific details on our strategy definitions are available in *Filtering Data and Grouping Permits into Strategies*.

**Diversity Index.** Our models focused on species diversity as a possible predictor of revenue and revenue variability while controlling for effort. For consistency with previous analyses (10, 13, 14, 29, 35, 43), we calculated effective species diversity for permit holder  $i$  and time (year)  $t$  as the inverse of Simpson’s concentration index  $\lambda$  (21, 22) [this index is also referred to in economics as the Herfindahl–Hirschman Index (44)] weighted by revenue  $R$ :

$$1/\lambda_{i,t} = 1 / \left[ \sum_{s=1}^{n_{i,t}} \left( R_{i,s,t} / \sum_{s=1}^{n_{i,t}} R_{i,s,t} \right)^2 \right],$$

where  $s$  indexes species from 1 through  $n$ .

We calculated effort or effective season length as the sum of the season lengths for each permit each year. Season length for a given permit was calculated as the number of days between the first instance of fishing a permit and the last instance of fishing a permit each year. For example, if an individual’s season lasted for 30 d on a salmon drift gillnet permit in southeast Alaska and 40 d on a statewide longline halibut permit, that individual’s season length was calculated as 70 d.

**Hierarchical Model.** To jointly model revenue and revenue variability as a function of individual-level covariates, we extended the basic variance function regression to a hierarchical Bayesian variance function regression model with Gaussian errors predicting log revenue,  $\log(R_{i,t})$ , for each fisher  $i$  and time  $t$ :  $\log(R_{i,t}) \sim \mathcal{N}(\mu_{i,t}, \sigma_{i,t}^2)$ .

Each year  $t$  of revenue for fisher  $i$  is assigned a strategy (permit set) indexed by  $j$  (Table S1), and  $\mu_{i,t}$  is modeled as

$$\begin{aligned} \mu_{i,t} = & \beta_{0,j,t} + \beta_{1,j}S_{i,t}I_{i,t} + \beta_{2,j}S_{i,t}I_{i,t} + \beta_3D_{i,t} \\ & + \beta_4S_{i,t}D_{i,t}I_{i,t} + \beta_5S_{i,t}D_{i,t}I_{i,t} + \log(R_{i,t-1}), \end{aligned} \quad [1]$$

where  $S_{i,t}$  is the log ratio of species diversity from year to year,  $\log(\text{div}_{i,t}/\text{div}_{i,t-1})$ ,  $D_{i,t}$  is the log ratio of days fished from year to year,  $\log(\text{days}_{i,t}/\text{days}_{i,t-1})$ , and  $I_{i,t}$  is an indicator variable that takes a value 0 if  $\text{div}_{i,t} \geq \text{div}_{i,t-1}$  (species diversity increasing year to year; generalizing) and takes a value 1 if  $\text{div}_{i,t} < \text{div}_{i,t-1}$  (species diversity decreasing year to year; specializing). Estimating a separate coefficient for the effect of increasing diversity and decreasing diversity allows the costs and benefits of these changes to be asymmetric.

We use  $\log(R_{i,t-1})$  as an offset, and thus our model describes the log ratio of revenue from year to year, i.e.,  $\log(R_{i,t}) - \log(R_{i,t-1}) = \log(R_{i,t}/R_{i,t-1})$ .

We model change in revenue because preliminary analyses revealed nonstationary trends in revenue (resulting from experience or other unmodeled factors). This approach reduces the nonstationarity of the time series and allows us to avoid estimating thousands of mean revenue intercepts associated with individual fishers. Because we were modeling year-to-year changes, we removed person-year combinations without a subsequent year of revenue.

The  $\beta$  terms represent estimated coefficients, some of which are allowed to vary as “random effect” terms. The intercepts  $\beta_{0,j,t}$  are allowed to vary by strategy-year combinations, are centered on zero, and are constrained by a normal distribution:  $\beta_{0,j,t} \sim \mathcal{N}(0, \sigma_{\beta_{j,t}}^2)$ .

This approach, combined with the lack of a global intercept, constrains the mean change in log revenue across all fishers and years to be zero, i.e., we assume that the data are stationary after accounting for all covariates and including an intercept that varies with strategy-year combinations. Initial versions of the model confirmed that the global intercept along with strategy-level intercepts would be estimated at almost exactly zero. The estimated  $\beta_{j,t}$  coefficients represent years when people with a particular set of permits tended to collectively do better or worse than the long-term average (Fig. S7). Therefore, an individual’s expected change in revenue (and variability) represents the expectation after accounting for the general trend in revenue for that set of permits.

The slopes  $\beta_{1,j}$  and  $\beta_{2,j}$  are then allowed to vary by strategy with estimated means:  $\beta_{1,j} \sim \mathcal{N}(\mu_{\beta_1}, \tau_{\beta_1}^2)$ ,  $\beta_{2,j} \sim \mathcal{N}(\mu_{\beta_2}, \tau_{\beta_2}^2)$ . The  $\beta_{1,j}$  and  $\beta_{2,j}$  coefficients represent how much a 1% decrease and 1% increase, respectively, in the ratio of species diversity from year to year within a strategy translates to a given percent change in the ratio of revenue from year to year. These are after controlling for changes in effort,  $\beta_3$ , and the interaction between changes in effort and changes in species diversity,  $\beta_4$  and  $\beta_5$ .

Whereas traditional hierarchical linear models assume homoscedasticity—that the residual variance does not vary systematically—our variance function regression model allows the residual variance to be heteroscedastic and vary as a function of predictors. Instead of estimating a single residual error scale term,  $\sigma$ , we model the scale of the residual error with another hierarchical model with a similar form,

$$\begin{aligned} \sigma_{i,t} = & \exp(\gamma_{0,j} + \gamma_{1,j}S_{i,t}I_{i,t} + \gamma_{2,j}S_{i,t}I_{i,t} + \gamma_3D_{i,t} \\ & + \gamma_4S_{i,t}D_{i,t}I_{i,t} + \gamma_5S_{i,t}D_{i,t}I_{i,t}). \end{aligned} \quad [2]$$

Again,  $S_{i,t}$  and  $I_{i,t}$  represent, respectively, the log ratio of species diversity from year to year and an indicator variable for increasing or decreasing species diversity. We exponentiate the equation to ensure that all scale parameters,  $\sigma_{i,t}$ , are positive. Residuals from the mean component of our model clearly show a “V”-shaped pattern, which the variance component of our model can capture (Fig. S8). Furthermore, the downside residuals (year-individual data points with lower than expected revenue) appear qualitatively similar to the complete set of residuals (upside and downside) (Fig. S9). Therefore, it seemed appropriate to model variability as a proxy for revenue risk. Ideally, we would model a more direct measure of risk, such as the probability of bankruptcy from low revenue; however, data on costs and other sources of income were not available.

The  $\gamma$  are estimated coefficients, three of which are allowed to vary by strategy, constrained by normal distributions,

$$\gamma_{0,j} \sim \mathcal{N}(\eta_0 + \eta_1M_j + \eta_2E_j, \tau_{\gamma_0}^2), \quad [3]$$

$$\gamma_{1,j} \sim \mathcal{N}(\mu_{\gamma_1}, \tau_{\gamma_1}^2), \quad \gamma_{2,j} \sim \mathcal{N}(\mu_{\gamma_2}, \tau_{\gamma_2}^2). \quad [4]$$

The  $\gamma_{0,j}$  coefficients are modeled with two strategy-level predictors. The symbols  $M_j$  and  $E_j$  represent the mean species diversity and mean combined fishing season length (effort) for strategy  $j$ . The coefficients  $\eta_1$  and  $\eta_2$  represent predictors in this strategy-level regression estimating effects across strategies.

We fit our models with Stan 2.14.1 (45, 46) and R 3.3.2 (47). Stan implements the No-U-Turn Hamiltonian Markov chain Monte Carlo algorithm (48) to perform Bayesian statistical inference. We assigned weakly informative priors on all parameters:  $\mathcal{N}(0, 2^2)$  priors on all  $\beta, \gamma$ , and  $\eta$  parameters, and half- $t(3, 0, 2)$  priors (i.e., degrees of freedom of 3 and scale of 2) on all  $\sigma$  and  $\tau$ . We ran four chains and 2,000 iterations and discarded the first 1,000 iterations of each chain as a warm-up. We checked for chain convergence visually with trace plots, and ensured that  $\hat{R} < 1.05$  (the potential scale reduction factor), and that the effective sample size, as calculated by the rstan R package (45), was >200 for all parameters (49). We verified that our model returned sensible estimates by comparing our estimates to an ad hoc two-stage model fit with the lme4 R package (50), where we first fit a mixed-effects regression model to the mean, and then modeled the absolute

residuals from that first model in a second mixed-effects model representing the variance component (*Model Checking with Two-Stage Approach*).

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