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Synergies in Coupled Human–natural Systems: Forty Years of Evidence for Biodiversity Recovery and Nature-based Economic Growth

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Abstract

Nature-based tourism is increasingly framed as a solution to the biodiversity crisis, yet the institutional and ecological conditions that ensure its long-term viability—particularly in the Global South—remain poorly understood. This study addresses this gap by analyzing the co-evolution of wildlife recovery, tourism dynamics, and governance trajectories through a knowledge co-production approach. Using a coupled human–natural systems framework, we examine nearly four decades (1987–2025) of whale-watching data in Península Valdés, Argentina, as part of a long-term socio-ecological research (LTSER) effort.

We quantify the non-consumptive economic value of the southern right whale (*Eubalaena australis*), estimating an individual asset value of USD 4.13 million, and assess whether intensifying tourism activity compromises population recovery. Our longitudinal analysis reveals that tourism and whale abundance have increased concurrently without evidence of mutual interference, facilitated by shared ecological drivers within a polycentric governance arrangement. We identify three systemic pillars for this synergy: (i) high ecological predictability; (ii) adaptive governance frameworks that manage spatial-temporal access; and (iii) economic structures that promote regional benefit-sharing.

Our findings challenge the assumption that tourism-led conservation is inherently sustainable, demonstrating instead that success is contingent upon deliberate institutional design. We argue that aligning economic incentives with conservation requires internalizing ecological feedback loops that safeguard planetary-scale services, such as blue carbon sequestration via the "whale pump." By providing rare empirical evidence from a developing economy, this research advances theoretical understanding of how nature-based economies can strengthen social-ecological resilience and serve as scalable models for sustainable development in an era of rapid environmental change.

1. INTRODUCTION

Nature-based economies are increasingly recognized as critical components of sustainable development pathways under global environmental change [1]. Across coastal regions worldwide, biodiversity not only underpins ecosystem functioning but also generates substantial economic value through non-extractive activities such as tourism [2]. Understanding how these nature-based economic systems interact with conservation outcomes is therefore central to advancing resilient socio-ecological systems in the face of accelerating environmental change.

A central challenge in this context lies in understanding how feedback between human and natural systems shape long-term outcomes. Research on coupled human–natural systems has highlighted that interactions between ecological dynamics, economic behavior, and institutional arrangements are often non-linear, context-dependent, and mediated by governance structures [3, 4]. From a resilience perspective, such systems are characterized by adaptive capacity and the potential for feedback to either stabilize or destabilize system trajectories under changing environmental conditions [5, 6]. As one of the fastest-growing sectors of the global economy, tourism based on wildlife and natural ecosystems

generates substantial economic benefits while simultaneously depending on ecological integrity. In marine systems, whale-watching represents a paradigmatic example of this interaction, linking the recovery of large marine vertebrates with expanding tourism economies. At the same time, the sustainability of such systems remains contested, as tourism activities may generate both positive and negative ecological impacts, depending on their scale, intensity, and governance context. Particularly, whale-watching tourism defined as commercial activities that allow the observation of cetaceans in their natural habitat [7], represents one of the most prominent and fastest-growing forms of marine nature-based tourism worldwide [8, 9]. Over recent decades, it has expanded across diverse geographic regions, generating substantial revenues, employment opportunities, and international visitation. Importantly, the economic footprint of whale-watching extends beyond direct expenditures, supporting broader sectors such as transportation, accommodation, and local services. This expansion has led to increasing interest in evaluating the economic value of cetaceans as non-consumptive natural capital, particularly in contexts where conservation and development objectives intersect [10, 9].

Large cetaceans exemplify this interface between ecological processes and economic systems. Beyond their ecological roles—including contributions to nutrient cycling and carbon sequestration through the whale biological pump [11, 12]—cetaceans provide a wide range of cultural ecosystem services linked to tourism, recreation, and environmental awareness [13]. Their global visibility and cultural significance position them as key providers of cultural ecosystem services, linking biodiversity conservation with local and regional economic development [14, 15, 13]. Despite increasing attention to the economic valuation of wildlife and ecosystem services, most existing studies adopt static approaches that do not fully capture the dynamic interactions between ecological processes, economic incentives, and institutional change. This limitation constrains our ability to understand whether nature-based economies can contribute to system resilience under conditions of global environmental change. There is a need for integrative, long-term analyses that explicitly examine how ecological recovery, tourism dynamics, and governance co-evolve over time, building on frameworks that link vulnerability, resilience, and coupled system dynamics [16, 17]. Empirical evidence that jointly examines ecological processes (e.g., whale abundance and distribution), tourism demand, and governance arrangements across scales is still limited, especially in the Global South. This lack of integrated and longitudinal analyses constrains the capacity to evaluate whether nature-based tourism can effectively align economic incentives with conservation outcomes over time, particularly in the face of climate variability, shifting species distributions, and evolving institutional contexts. Addressing these gaps requires interdisciplinary approaches that explicitly account for cross-scale interactions, governance complexity, and the co-evolution of social and ecological systems [18, 19, 20].

Building on these gaps, this study aims to advance understanding of whale-watching as a coupled social–ecological system under conditions of global environmental change. Specifically, it seeks to integrate ecological dynamics, tourism demand, and governance frameworks within a unified analytical approach, to examine how interactions between these dimensions shape system outcomes over time. By focusing on Península Valdés (Argentina), a UNESCO World Heritage Site that hosts one of the most important breeding populations of southern right whales (*Eubalaena australis*) experiencing sustained

growth in tourism activity alongside the recovery of whale populations, the paper provides empirical evidence on the relationships between whale abundance, patterns of tourism activity, and the role of regulatory and institutional arrangements in mediating these interactions. Particularly, the study adopts a coupled human–natural systems perspective to conceptualize whale-watching in Península Valdés as a dynamic socio-ecological system shaped by interactions among ecological processes, economic activities, and governance structures. Leveraging a unique combination of ecological data, tourism statistics, and historical records spanning nearly four decades (1987–2025) using long-term socio-ecological research (LTSR), we integrate three key dimensions: (i) ecological dynamics, including whale abundance and mortality events; (ii) tourism demand and economic flows associated with whale-watching; and (iii) institutional and governance arrangements that regulate access, manage impacts, and distribute benefits.

Specifically, this study addresses the following research questions: (1) How have whale-watching activities and associated tourism dynamics evolved over recent decades in Península Valdés, and what does this reveal about the long-term development of nature-based economies?; (2) What is the non-consumptive economic value of southern right whales (*Eubalaena australis*) at both individual and population levels, and how does this value contribute to regional economic systems?; (3) To what extent are ecological dynamics (e.g., whale abundance) associated with patterns of tourism demand, and what implications does this have for system resilience under environmental change?; (4) how do governance arrangements mediate interactions between ecological and economic processes?

Unlike traditional academic assessments, this study utilizes a transdisciplinary co-production approach [21], integrating perspectives from academia, local government, and the private tourism sector (including tour operators and hospitality federations). By linking long-term empirical evidence with a coupled systems perspective, this study advances understanding of how feedback between biodiversity, economic activity, and governance shape the resilience of nature-based economies under global environmental change. More broadly, it contributes to ongoing debates on the role of biodiversity-based systems in sustainable development, highlighting the conditions under which conservation and economic objectives may co-evolve.

2. MATERIALS AND METHODS

2.1 Study Area

Península Valdés Natural Protected Area (Patagonia, Argentina) serves as a representative coastal socio-ecological system (SES) to examine the linkages between ecological variability, economic behavior, and governance frameworks. Designated as a UNESCO World Heritage Site, the region supports one of the most significant breeding populations of southern right whales (SRWs) in the Southwestern Atlantic. The study area encompasses Golfo Nuevo, specifically focusing on whale-watching operations based in Puerto Pirámides (Fig. 1). This coastal village (~ 700 inhabitants) is the sole authorized port in Chubut Province for whale-watching excursions. Located within the Península

Valdés, Puerto Pirámides is situated 100 km from the regional urban and logistical hub of Puerto Madryn. Access to the site is regulated via Provincial Route No. 2, where the Administration of the Península Valdés Protected Area (AANPPV) manages entry and collects visitation fees, representing a key institutional actor in the local governance structure.

2.2 Methodology

To address the research objectives, we implemented a multi-stage analytical framework integrating ecological, economic, and governance dimensions within a coupled human–natural systems perspective (Fig. 2). Economic data and institutional trajectories were validated through direct collaboration with key stakeholders in the regional tourism value chain, ensuring that the valuation reflects actual operational dynamics and indirect expenditure patterns. This transdisciplinary approach ensures that the identified feedback loops are grounded in operational realities, facilitating the adaptive management required under global environmental change [22]. First, we estimated the non-consumptive economic value of SRWs for the year 2024, quantifying both direct and indirect economic contributions derived from whale-watching. This valuation captures the role of cetaceans as natural capital generating high economic value through non-extractive use.

Second, we reconstructed the development of whale-watching activity in Península Valdés through long-term socio-ecological research (LTSER) over the period 1987–2025. This reconstruction integrates multiple data sources, including tourist numbers, excursion pricing, and annual estimates of SRW abundance, enabling the identification of long-term trajectories in both tourism growth and ecological dynamics. This step allows for assessing whether sustained tourism expansion has occurred alongside stable or increasing whale populations.

Third, we evaluated the relationship between tourism intensity and whale abundance using generalized additive models (GAMs). GAMs were selected due to their ability to handle the non-linearities and temporal dependencies inherent in decadal socio-ecological datasets. This analysis provides empirical evidence on whether increasing tourism pressure is associated with negative ecological effects.

Together, these components enable the assessment of three key dimensions: (i) the magnitude and distribution of economic benefits derived from whale-watching, including indirect spillover effects; (ii) the long-term co-evolution of ecological and tourism dynamics; and (iii) the extent to which governance frameworks mediate these interactions. By integrating these dimensions, the methodological approach provides a basis for evaluating system resilience and the role of adaptive governance in sustaining nature-based economies under global environmental change.

2.3 Estimation of the SRW non-consumptive economic value

The individual economic value (IEV), annual individual economic value ($IEV\prime$), and population economic value (*PEV*), were estimated following the equations proposed by [23]. All fees originally expressed in Argentine pesos (AR$) were converted to U.S. dollars (USD) using the official exchange rate

up to October 2011 and, thereafter, the informal exchange rate in Argentina [24, 25], based on monthly average values obtained from Ámbito Financiero (https://www.ambito.com/; accessed in October 2025).

$$Eq.\ 1.\ IEV = \frac{(DE + IE)\ .\ MA}{N}$$

$$Eq.\ 2.\ IEV\prime = \frac{IEV}{MA}$$

$Eq.\ 3.$ *PEV = IEV. N*

where DE is the direct expenditure, IE is the indirect expenditure, MA is the average whale age, and *N* is the average number of SRW. Each of the economic parameters involved in the calculation of these equations was described in greater detail below.

2.3.1 Direct expenditure ($\varvec{DE}$)

Direct expenditure was determined as the sum of two components: the cost associated with whale-watching boarding pass (WW) and the entrance fee to the Península Valdés (PV). The $WW$was calculated as the sum of the product between the number of tourists (t) participating in the activity during the June–December season and the corresponding monthly (m) fees for children (cp) and adults (ap). This calculation accounted for the typical composition of whale-watching tourist groups, in which 31.7% of participants are minors and the remaining 68.3% are adults [26]

$$Eq.\ 4.\ WW = \sum_{m=Jun}^{Dec} t_m\ .\ (0.317cp_m + 0.683ap_m)$$

To estimate PV, the Administration of the Península Valdés Natural Protected Area provided data on the origin and number of tourists visiting the area during the whale season, as well as monthly entrance fees (M. Eugenia Vall, Administración del Área Natural Protegida Península Valdés, pers. comm., 1 October 2025). Using these data, the monthly proportions of foreign, domestic, and Chubut-resident tourists entering the area during the whale season (June–December) was calculated. These proportions were then extrapolated to the total number of tourists participating in whale-watching activities in Puerto Pirámides [26].

$$Eq.\ 5.\ PV = \sum_{i=1}^{S} \sum_{m=Jun}^{Dec} t_{i,m}\ e_{i,m}$$

where S is the total number of tourist segments *(i.e.*, each combination of tourist category —origin— and age subcategory —children and adult), i is the index representing each tourist segment, m denotes the month of the whale season (June–December), $t_{i,m}$ is the number of tourists in segment i during month m, and $e_{i,m}$ is the corresponding fee for segment i in month m.

2.3.2 Indirect expenditure ($\varvec{IE}$)

Indirect expenditure was calculated as the sum of two components: travel costs (TC) and accommodation cost (AC). To estimate TC associated with whale-watching, we considered 100% of foreign tourists, 88.4% of domestic tourists, and 98.52% of residents of the Chubut province who traveled by car, airplane, or bus to the city of Puerto Madryn [26] (Supplementary Fig. S1), which represents the closest and most important tourism hub to the town of Puerto Pirámides. For domestic flights taken by foreign tourists, expenditure was estimated proportionally based on 13,901 passengers, who accounted for 3.7% of the total revenue generated by inbound tourism in Argentina during 2024 (USD 13,177 million) [27]. To this amount, we added to the additional cost of ground transportation from Puerto Madryn to Puerto Pirámides, corresponding to the transfer service offered by local tourism agencies (Giselle Tschopp, Argentina Visión, pers. comm., 30 July 2025). Considering the typical composition of whale-watching tourist groups [26] and the differential pricing structure of transfer services, it was assumed that 31.7% of foreign tourists (*f*) paid the child transfer fee (*ct*), while the remaining proportion paid the adult transfer fee (*at*). Accordingly, the expenditure by foreign tourists (*EF*) was defined as:

$$Eq.6.\ EF\ =\ 487.573 + f\ .\ (0.317ct + 0.683at)$$

For domestic tourism, we considered the provinces of Córdoba, Río Negro, Mendoza, Santa Fe, Tucumán, and Buenos Aires, identified as the main tourist source regions [26]. The expenditure made by domestic tourists traveling by air (EDp) was calculated as the product of the number of domestic tourists using this mode of transport (dp) and the associated airfare cost (pc). As for international tourism, an additional ground transportation cost from Puerto Madryn to Puerto Pirámides was included, corresponding to transfers provided by local tourism agencies and considering the proportion of child and adult tourists participating in whale-watching activities [26]. Accordingly, the expenditure by domestic tourists associated with air travel was calculated as:

$$Eq.7.\ EDp\ =\ dp.\ pc\ + dp\ .\ (0.317ct + 0.683at)$$

Analogously, the expenditure of domestic tourists traveling by bus (EDb) was calculated based on the number of passengers using this transport mode (db), the associated bus fares (bc), and the transfer service fees from Puerto Madryn to Puerto Pirámides.

$$Eq.\ 8.\ EDb\ =\ db.\ bc + db\ .\ (0.317ct + 0.683at)$$

The expenditure associated with domestic tourists traveling by car (EDc) was estimated as the product of the number of domestic tourists using this transport mode (dc) and the corresponding travel costs (cc), divided by 3.5 to reflect the average travel group size [26]. EDc was therefore calculated as follows:

$$Eq.9.\ EDc\ =\ \frac{dc\ .\ cc}{3.5}$$

For resident tourism of Chubut, two alternative travel scenarios were considered. The first corresponds to the expenditure associated with bus travel (ERb), calculated as the product of the number of resident tourists who used this transport mode (rb) and the average ticket cost ($\bar{bc}$) from the main cities of the province (*i.e.*, Esquel, Comodoro Rivadavia, and Trelew) to Puerto Madryn. In addition, the analysis uses the supplementary cost of ground transfers operated by tourism agencies from Puerto Madryn to Puerto Pirámides, including both adult and child fares.

$$Eq.\ 10.\ ERb = \ rb\ .\ \bar{bc} + rb\ .\ (0.317ct + 0.683at)$$

The second alternative considers the expenditure associated with travel by private car (ERc). This was calculated as the product of twice the average distance between the main tourist centers of Chubut and the city of Puerto Pirámides ($\bar{x}$) and the average fuel cost (gc), defined as the mean price of regular gasoline in 2024, obtained from the Confederation of Entities of the Hydrocarbon and Related Products Trade of Argentina (http://cecha.org.ar/, accessed September 2025). The calculation assumes the fuel efficiency of a standard passenger vehicle under highway conditions (*i.e.*, 10 L per 100 km). This value was subsequently divided by 3.5 to account for the average size of a tourist travel group and its shared economic contribution [26]:

$$Eq.\ 11.\ ERc = \frac{2\ \bar{x}.\ gc}{3.5}$$

Based on all the parameters estimated above, the travel cost (TC) was defined as follows:

$$Eq.\ 12.\ TC = \ EF + EDp + EDb + EDc + ERb + ERc$$

Finally, accommodation expenses (AE) included tourist expenditures in seven hotels of different categories (*i.e.*, 2- to 5-star hotels) and short-term rental apartments located in the city of Puerto Madryn (Angelica Crusate, Red de Alquileres Temporarios de Puerto Madryn, pers. comm., 11 November 2025). The relative contribution of each accommodation type to the estimated average expenditure was weighted according to occupancy rates. Accordingly, AE was defined as follows:

$$Eq.\ 13.\ AE = \ t.\ (\ \bar{h} \cdot w_h + \bar{d} \cdot w_d)$$

where t is the number of tourists who participated in whale-watching activities, $\bar{h}$ is the average cost of hotel accommodation and w_h its relative weight, $\bar{d}$ is the average cost of short-term rental accommodation and w_d its relative weight.

2.4 SRWs population data: abundance and mean age

We modeled the monthly abundance of SRWs between 1999 and 2024 using a Generalized Additive Model (GAM) with a negative binomial error distribution and a log link function, implemented with the *mgcv* package in R [28] (Supplementary Fig. S2). GAMs allow for the identification of nonlinear

relationships between abundance and month, providing a more realistic representation of seasonal fluctuations [29, 30, 31]. The use of a negative binomial distribution accounts for variance exceeding the mean (overdispersion), thereby reducing bias in standard error estimates and in the statistical significance tests of relationships among variables [31]. Abundance data for the period 1999–2021 were obtained from [32], while data for the 2021–2024 period were supplemented with aerial surveys conducted by the Marine Mammal Laboratory (LAMAMA–CESIMAR). The variable *month* was included as a cyclic cubic spline to represent seasonality in the number of individuals, and a population growth offset was incorporated to control for interannual changes in abundance. This offset assumed an annual growth rate of 6.5% for the period 1999–2011 and 3.15% per year for the period 2012–2024 [32]. Finally, the average whale abundance during 2024 was 737 individuals and the average whale age of 73.4 years was adopted based on estimates reported by [33].

2.5 Information sources and historical reconstruction of whale-watching

Two data sources were used in this part of the study:

- Official documentation. Information on the number of tourists and the modes of travel used during the study period was obtained from official documents published by the Government of Chubut in the Tourism Statistical Yearbook 2023–2024 [26].
- Local whale-watching companies. The six whale-watching companies currently operating in Puerto Pirámides were invited to participate in this study, although only two agreed to collaborate. These companies provided detailed information on the pricing schemes applied to whale-watching activities throughout the study period. This information was integrated with SRWs abundance data derived from the GAM model, the number of tourists participating in the activity, and excursion costs over time, enabling a historical reconstruction of whale-watching activity. In addition, the companies provided information on key milestones in the development of the activity within the study area *(e.g.*, the onset of whale-watching, animal-approach practices, and the enactment of laws and regulations), which allowed for the interpretation of observed historical changes

2.6 Relationship between the number of tourists and SRWs

Trend analysis was conducted to assess whether there was a significant change in SRWs abundance as a function of the number of tourists, using Kendall's tau correlation coefficient (Kendall's τ), a non-parametric measure commonly applied to evaluate associations between variables in time-series data. According to [34], an absolute Kendall's τ value ≥ 0.5 indicates a strong trend; values between 0.3 and 0.5 indicate a moderate trend; and values between 0.1 and 0.3 indicate a weak trend. Because this test does not account for the temporal structure of the data nor allows for the assessment of complex non-linear relationships, a generalized additive model (GAM) with a negative binomial distribution was subsequently applied to identify the association between tourist numbers and SRW abundance, including time as a linear covariate.

3. RESULTS

3.1 Economic magnitude and structure of whale-watching benefits

In 2024, the estimated individual economic value (IEV) reached USD 4.13 million (USD 2.64–6.86 million), with an annual individual value ($IEV\prime$) of USD 56,238.95 (USD 29,938.52–114,384.42). At the population level, total economic value (PEV) exceeded USD 3.04 billion (USD 1.41–6.46 billion).

Economic contributions were strongly dominated by indirect expenditures, which totalled USD 41.47 million compared to USD 8.43 million in direct expenditures. Thus, approximately 83% of the total economic value was generated through indirect channels, primarily travel and accommodation. This cross-sectoral distribution indicates that the economic significance of whale-watching extends well beyond the core activity, permeating multiple sectors of the regional economy. This systemic integration suggests a high degree of economic diversification, which enhances the resilience of the socio-ecological system by buffering it against sector-specific fluctuations and amplifying its overall regional impact.

3.2 Long-term co-evolution of tourism and ecological dynamics

3.2.1 Growth trajectories

Whale-watching activity in Península Valdés has experienced sustained expansion over the study period (1987–2025), increasing from 5,214 recorded tourists in 1987 to 95,197 in 2024. Over the same period, SRW abundance exhibited a consistent recovery trajectory, reflecting long-term population growth. These parallel trends indicate a co-occurring expansion of both ecological and economic components. Crucially, the data shows a successful decoupling of tourism growth from environmental degradation, as the nearly twenty-fold increase in visitors did not halt or reverse the biological recovery of the species, suggesting a system operating within sustainable thresholds.

3.2.2 Institutional phases and system reconfiguration

The development of whale-watching can be characterized by three distinct institutional phases. An initial phase of unregulated growth (1970s–early 1980s) was followed by the introduction of formal regulations during the 1980s (Provincial Law No. 2,381), including licensing systems and early operational controls. In this context, whale-watching began to be institutionally formalized as a tourism activity in 1983, with the enactment of Provincial Law No. 2,381, which established the regulatory framework for service provision [35]. In 1984, the first regulations governing vessel approaches to marine wildlife were introduced to enhance protection for SRWs. That same year, SRWs were declared a Natural Monument in Argentina (National Law No. 23,094). In 1987, the number of passengers

participating in whale-watching excursions was officially recorded for the first time, reaching a total of 5,214 individuals [36].

A third phase, beginning in the early 2000s and consolidated in 2008, reflects the transition toward a structured polycentric governance regime, including standardized operational practices and the implementation of best-practice guidelines. The economic and financial crisis that affected Argentina in 2001 marked a turning point, prompting whale-watching companies to organize collaboratively to optimize economics returns and increase sectoral stability. This process culminated in 2008 with the enactment of the Whale-Watching Law and the implementation of the Patagonian Whale-Watching Technique and the Code of Good Practices (Provincial Law No. 5714, later Law No. XI-44, and its implementing decrees).

This phase led to the implementation of standardized best-practice guidelines and a multi-level management approach, creating the institutional buffer necessary to maintain system stability despite increasing global and local pressures.

3.2.3 System stabilization

Following the establishment of a more formalized regulatory framework, tourism dynamics became more consistent and predictable (with a total of 95,197 tourists recorded in 2024) [26]. The combination of increasing tourist numbers and sustained whale population growth suggests that the system has reached a phase characterized by relative stability, in which both ecological and economic components continue to expand within a regulated context.

3.3 Relationship between tourism pressure and whale population dynamics

The Kendall rank correlation revealed a weak but significant positive association between tourist numbers and whale abundance ($\tau = 0.22$, $p < 0.001$), indicating that increases in tourism have not been associated with declines in whale population size. Results from the generalized additive model (GAM) further support this pattern. The model identified a significant non-linear relationship between tourist numbers and whale abundance (edf = 4.73, $\chi^2 = 58.97$, $p < 0.001$), as well as a significant effect of time ($z = 4.16$, $p < 0.001$). The model explained 30.6% of the deviance (adjusted $R^2 = 0.53$), indicating moderate explanatory power. Overall, these results show no evidence of a negative relationship between tourism intensity and whale abundance over the study period. Instead, both variables appear to follow partially shared temporal dynamics, likely influenced by seasonal and long-term ecological processes.

3.4 Emergent properties of the coupled human–natural system

The integration of economic, ecological, and institutional results reveals several emergent properties of the whale-watching system in Península Valdés (Fig. 3). First, tourism expansion and whale population recovery appear to be decoupled from negative ecological impacts at the observed scale, as increasing

tourist numbers were not associated with declines in whale abundance (Fig. 4). Second, the economic structure of the system is characterized by strong indirect effects, with most of the economic value generated outside the immediate activity. This indicates that the benefits of biodiversity are distributed across a broader regional economy. Third, the co-evolution of tourism and ecological dynamics is closely associated with the progressive consolidation of governance frameworks. The temporal alignment between institutional strengthening and system expansion suggests that governance plays a central role in mediating interactions between ecological processes and economic activity. Together, these patterns highlight that system-level outcomes are not solely determined by ecological or economic dynamics in isolation but emerge from their interaction within a structured institutional context.

4. DISCUSSION

4.1 Nature-based economies as emergent system properties of socio-ecological health

Our findings demonstrate that the economic value of whale-watching in Península Valdés, estimated at USD 4.13 million per individual whale, is not a static financial metric but an emergent property of a functioning coupled human–natural system (CHNS). The magnitude of the estimated value exceeds previous global benchmarks that aggregate multiple ecosystem services [37], suggesting that even narrowly defined, non-consumptive uses can represent substantial economic assets. This valuation reflects the successful recovery of SRW population over four decades. Unlike consumptive uses of marine resources, where value is derived from extraction, the nature-based economy in the study area relies on the maintenance of ecological integrity. Importantly, the dominance of indirect expenditures indicates that the benefits of whale-watching extend far beyond the activity itself, permeating sectors such as transportation and accommodation. This amplification effect reinforces the idea that nature-based economies operate through cascading economic linkages, and that tourism-based valuations likely underestimate the full contribution of SRW to human well-being.

Furthermore, this economic success has profound implications for global climate stability. As highlighted [38, 39], the recovery of whales facilitates the "whale pump" mechanism, enhancing nutrient cycling and oceanic carbon sequestration. By quantifying the high resolution of these economic flows, we provide evidence that protecting individual whales not only supports regional prosperity but also safeguards critical ecosystem services for planetary resilience. Then, by fostering economic incentives for the protection of these populations, nature-based tourism indirectly safeguards a biological mechanism of global climate mitigation. Consequently, the Peninsula Valdés whale-watching industry transcends its role as a regional development engine, functioning as a socio-economic buffer that supports planetary-scale carbon sequestration services through whale’s ecological role [12]. This perspective reinforces the idea that nature-based economies, when properly regulated, do not merely exploit local 'amenities' but actively contribute to the maintenance of Earth System stability and global resilience."

4.2. Beyond trade-offs: Co-evolution and the decoupling of growth and impact

A central debate in sustainability science is whether tourism growth inevitably leads to ecological degradation [40, 41]. Our long-term analysis (1987–2025) provides a compelling counter-narrative, showing a synchronous expansion of both tourist numbers and whale abundance. This suggests a socio-ecological decoupling, where the system has been managed to avoid the typical "tragedy of the commons" often seen in unregulated nature-based tourism. This co-evolutionary trajectory was made possible by the transition toward polycentric governance. As shown in our GAM results (Fig. 4), the absence of a negative threshold effect—even with nearly 100,000 annual visitors—indicates that the institutional framework has successfully mitigated potential disturbance. The collaborative organization of local operators post-2001 (Section 3.2.2) transformed individual competition into a collective effort to maintain the quality of the "natural capital," effectively buffering the system against macroeconomic shocks and ecological variability.

However, rather than reflecting a simple “win–win” relationship, these dynamics are better understood as the outcome of partially coupled processes shaped by shared temporal drivers. The absence of a negative relationship between tourism intensity and whale abundance suggests that tourism growth has not constrained population recovery at the observed scale. Instead, both variables appear to respond to broader ecological and seasonal dynamics, highlighting the importance of distinguishing between correlation and causation in socio-ecological systems.

This pattern contrasts with the more commonly documented trade-offs between tourism expansion and ecological degradation, suggesting that, under specific conditions, nature-based economies may operate as stabilizing rather than destabilizing forces. At the same time, recent research highlights that tourism systems can simultaneously generate both positive and negative feedbacks, reinforcing the need to move beyond simplified win–win narratives [42, 43].These findings support a growing body of literature emphasizing that outcomes in human–environment interactions are not solely determined by ecological or economic drivers, but by the institutional configurations that structure their relationships [44, 4]. In this context, governance acts as a critical lever that can either amplify or dampen feedback between biodiversity and economic systems, particularly under conditions of global change where multi-level coordination and institutional flexibility are essential [45]. However, the replicability of this stabilizing feedback depends on specific 'boundary conditions' inherent to the Península Valdés system. Moreover, the collaborative nature of this research—involving scientists, local regulators, and private operators—is a testament to the high social capital and institutional maturity of the Península Valdés system, which facilitates the rapid feedback loops necessary for adaptive management.

The coastal and highly predictable nature of southern right whales facilitates a level of spatial-temporal regulation that may be harder to achieve in more fluid or remote ecosystems. For instance, while our model’s pillars—ecological predictability and robust governance—could theoretically be exported to cases like gorilla trekking in Rwanda (high predictability, high regulation), they might face significant

challenges in more fugitive or open-ocean systems, such as shark-diving in Fiji or pelagic birdwatching. By acknowledging that the southern right whale is an ecologically 'tractable' species for regulation, we emphasize that the success of nature-based economies is not a universal guarantee, but a strategic outcome of matching institutional design with the specific biological traits of the focal species. This distinction is vital for global conservation policy: sustainable development pathways are most resilient when governance structures are custom-tailored to the ecological rhythms of the natural capital they aim to protect. This suggests that the absence of trade-offs is not a default ecological state, but a managed outcome that requires a specific institutional architecture to persist.

4.3. Polycentric governance as a driver of system stability

Building on the empirical evidence of co-evolution, we argue that this stability is a deliberate outcome of a polycentric governance arrangement [4]. In Península Valdés, the interaction between provincial agencies, academic researchers, and local private stakeholders—including the hospitality and tour operating sectors represented in this study—creates a multi-layered institutional structure.

This bottom-up engagement is critical for system resilience; it ensures that regulatory compliance is driven by a shared economic interest in the health of the whale population, rather than merely by external sanctions. As suggested by [46], such polycentric systems are often more effective at managing common-pool resources because they allow for faster feedback loops and greater 'institutional fit' with the local ecological rhythms. In this context, the private sector acts as a distributed monitoring network, where operators and hospitality providers become de facto stewards of the resource. This decentralized oversight provides the adaptive capacity needed to adjust tourism intensity in real-time, buffering the system against the socio-ecological uncertainties of global environmental change.

4.4 Beyond Península Valdés: Scaling and transferability of the CHNS model

Our findings underscore that the observed synergy between conservation and development is not a product of top-down command-and-control regulation alone, but rather the result of a polycentric governance arrangement [4]. In Península Valdés, the interaction between provincial enforcement agencies, academic researchers, and local private stakeholders—ranging from boutique hotels to specialized tour operators—creates a multi-layered institutional structure. This bottom-up engagement is critical for system resilience; it ensures that regulatory compliance is driven by a shared economic interest in the health of the whale population, rather than merely by external sanctions. As suggested by [46], such polycentric systems are often more effective at managing common-pool resources because they allow for faster feedback loops and greater 'institutional fit' with the local ecological rhythms. In this context, the private sector acts as a distributed monitoring network, where operators and hospitality providers become de facto stewards of the resource. This decentralized oversight provides the adaptive capacity needed to adjust tourism intensity in real-time, buffering the system against the socio-ecological uncertainties of global environmental change.

The identification of polycentric governance as a stabilizing lever suggests that the Península Valdés model is not merely a geographic exception, but a scalable framework for nature-based economies elsewhere. However, the transferability of these lessons—to contexts such as shark-diving in Fiji or gorilla trekking in Rwanda—depends on the alignment between institutional design and specific 'boundary conditions.'

Our analysis identifies two critical factors for replicability: a) Ecological Tractability: the coastal and highly predictable site-fidelity of southern right whales facilitates spatial-temporal regulation that may be harder to achieve in open-ocean or fugitive systems; and b) Institutional Fit: the success of the Península Valdés model relies on the capacity of local networks to internalize ecological feedbacks. As we have shown, when governance is custom-tailored to the ecological rhythms of the focal species, nature-based tourism transcends its role as a simple industry. It becomes a reproducible strategy for maintaining Earth System stability, linking local economic incentives with global services like carbon sequestration.

4.5 Resilience under global environmental change

While the Península Valdés system has demonstrated remarkable adaptive capacity, its long-term resilience is not guaranteed. The "win-win" dynamics observed over the last four decades remain contingent on the system's ability to buffer cumulative and synergistic stressors. As argued by [47], multidimensional resilience in tourism social-ecological systems is not a static property but a dynamic interplay between biodiversity signals and economic shocks. Our findings suggest that the stability of nature-based economies depends on the maintenance of ecological predictability; however, this predictability is increasingly threatened by external drivers. A substantial body of literature documents behavioural and physiological responses of cetaceans to vessel interactions, particularly in sensitive groups such as mother–calf pairs [48, 49, 50]. Although current regulatory frameworks appear effective in maintaining impacts within sustainable bounds, the long-term resilience of the system remains contingent on its ability to buffer cumulative effects. These may arise not only from increasing tourism pressure or declining compliance [51, 52] but also from a broader context of interacting stressors. In Península Valdés, the convergence of disease outbreaks [53], harmful algal blooms [54, 55], and climate-driven environmental change [56] creates a 'synergistic vulnerability' that may erode the system's adaptive capacity. These dynamics highlight that resilience is inherently dynamic and contingent, requiring adaptive governance—rather than static management—to navigate the increasing uncertainty of global environmental change.

To navigate these risks, the polycentric governance described in section 4.3 must evolve from static management to anticipatory governance. This requires integrating real-time environmental monitoring with flexible economic policies that can absorb periods of low whale abundance without collapsing the regional social fabric. Resilience, therefore, is not a state to be reached, but a dynamic process of continuous adjustment to the escalating uncertainties of the Anthropocene.

4.6. Policy Implications for the Global South

The broader significance of this work lies in challenging the persistent dichotomy between biodiversity conservation and economic development. By framing nature-based economies as emergent properties of coupled systems, we provide a roadmap for the Global South to treat natural capital not as a luxury, but as a structural foundation for regional stability. The "Peninsula Valdés Model" offers a scalable blueprint for other emerging economies. It proves that prioritizing the recovery of natural capital is not a luxury but a strategic investment in regional stability. For policymakers, the lesson is clear: long-term ecological monitoring coupled with adaptive, collaborative institutions is the most effective safeguard for nature-based economies in an era of increasing environmental uncertainty.

Future research should focus on how these regional successes can be integrated into international blue carbon credit markets, further bridging the gap between local conservation and global climate finance.

Declarations

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Author Contribution

F.M.H.: Conceptualization; data curation, formal analysis; investigation; methodology; software; writing — original draft, review and editing.

A.C.: Data curation; methodology; validation; writing- review & editing.M.F.: Methodology; validation; writing- review & editing.

H.R and R.O: Methodology; resources; validation; writing- review & editing.

R.J.R.: Conceptualization; investigation; supervision; validation; visualization; writing — review and editing.

L.G.E: investigation; supervision; validation; visualization; writing — review and editing.

R. L.: Conceptualization; investigation; supervision; validation; visualization; writing — review and editing.

All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability

The primary tourism dataset used in this study, including the number of tourists, tourist origin, age composition, transportation mode, average travel group size, and participation in whale-watching activities, is publicly available through the Ministry of Tourism and Protected Areas of Chubut (2024) at: https://chubutpatagonia.gob.ar/wp-content/uploads/2025/06/AET-Chubut-2024-25.pdf. Additional publicly available tourism statistics were obtained from the National Institute of Statistics and Census (INDEC): https://www.indec.gob.ar/indec/web/Institucional-Indec-InformesTecnicos-55.The datasets generated and/or analysed during the current study are available upon request by contacting the corresponding author

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Figures

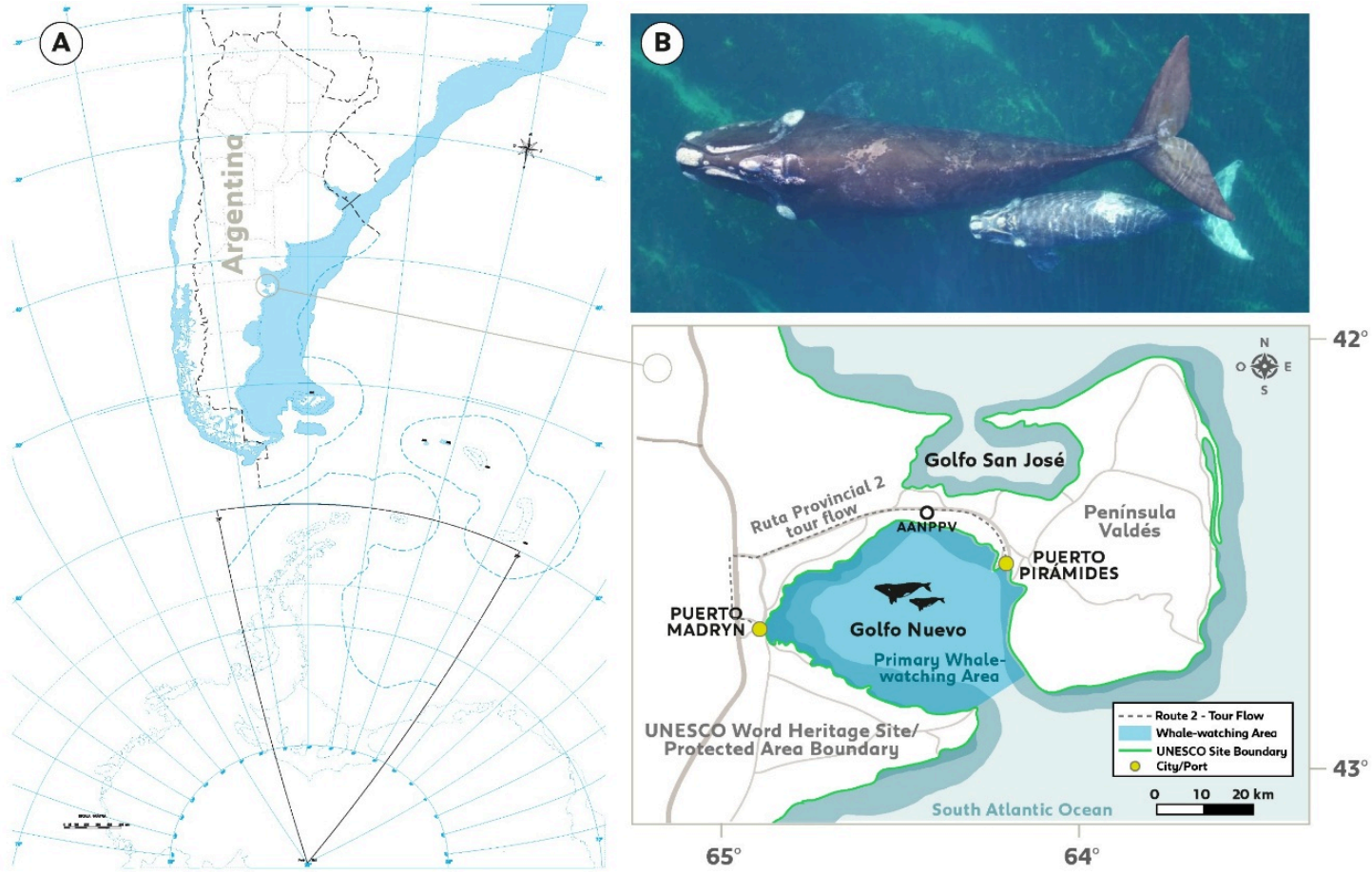


Figure 1

The Península Valdés Socio-Ecological System (SES). (Top Left) Regional context in Argentina. (Top Right) Detailed view of the study area, highlighting the logistical hub (Puerto Madryn) and the specialized whale-watching port (Puerto Pirámides) within the UNESCO World Heritage site. (Bottom) Southern right whale (*Eubalaena australis*) mother and calf, the core natural capital of the region's nature-based economy. The map was created in QGIS 3.12 (https://www.qgis.org/es/site/) and the final figure edition was generated using Photopea online graphics editor (https://www.photopea.com/).

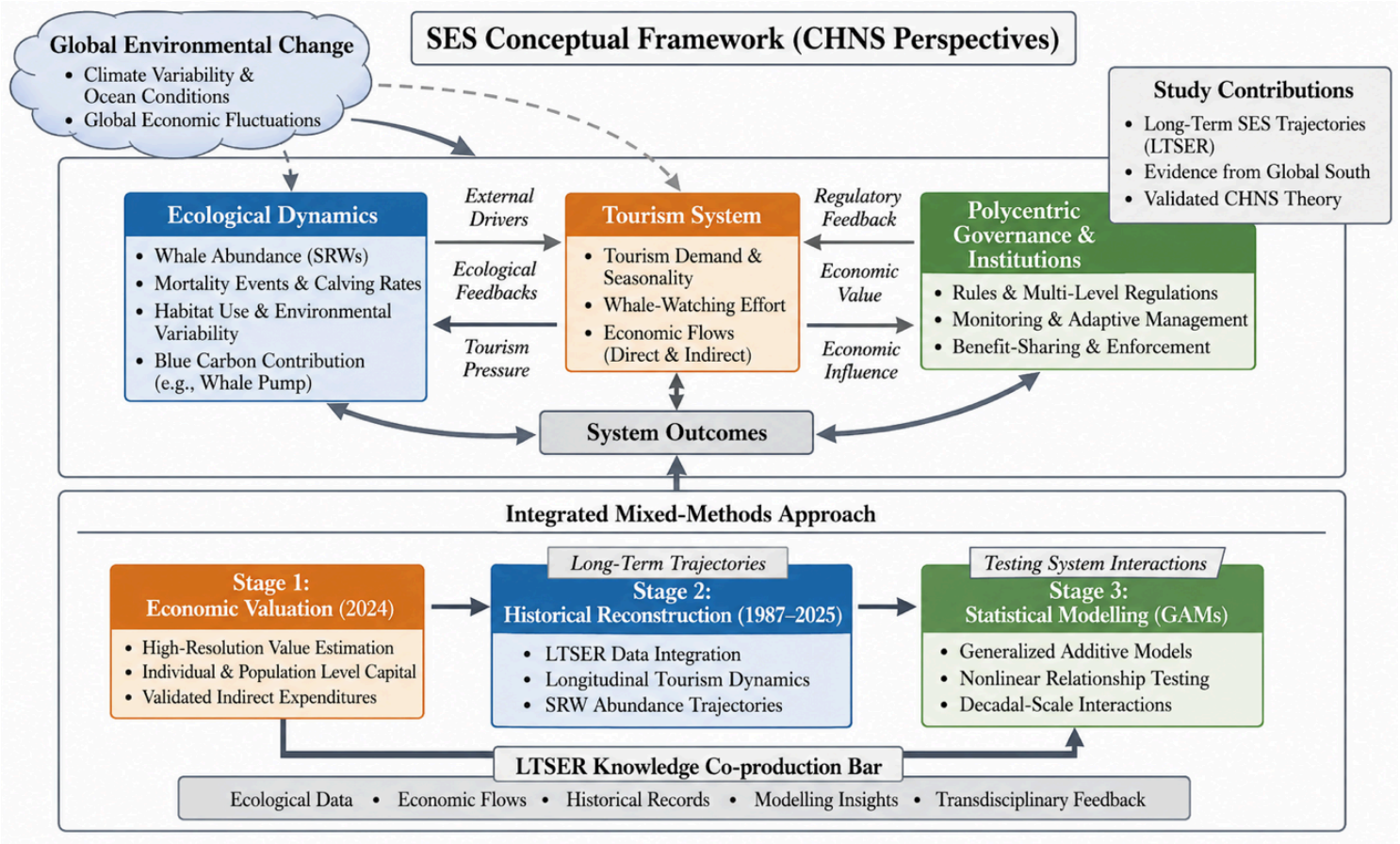


Figure 2

Integrated Socio-Ecological Research Framework. The upper panel illustrates the coupled human-natural system (CHNS) under global environmental pressures, highlighting the feedback loops between ecological dynamics, the tourism economy, and polycentric governance. The lower panel details the three-stage mixed-methods approach used to quantify economic value, reconstruct long-term trajectories (1987-2025), and test non-linear interactions using Generalized Additive Models (GAMs).

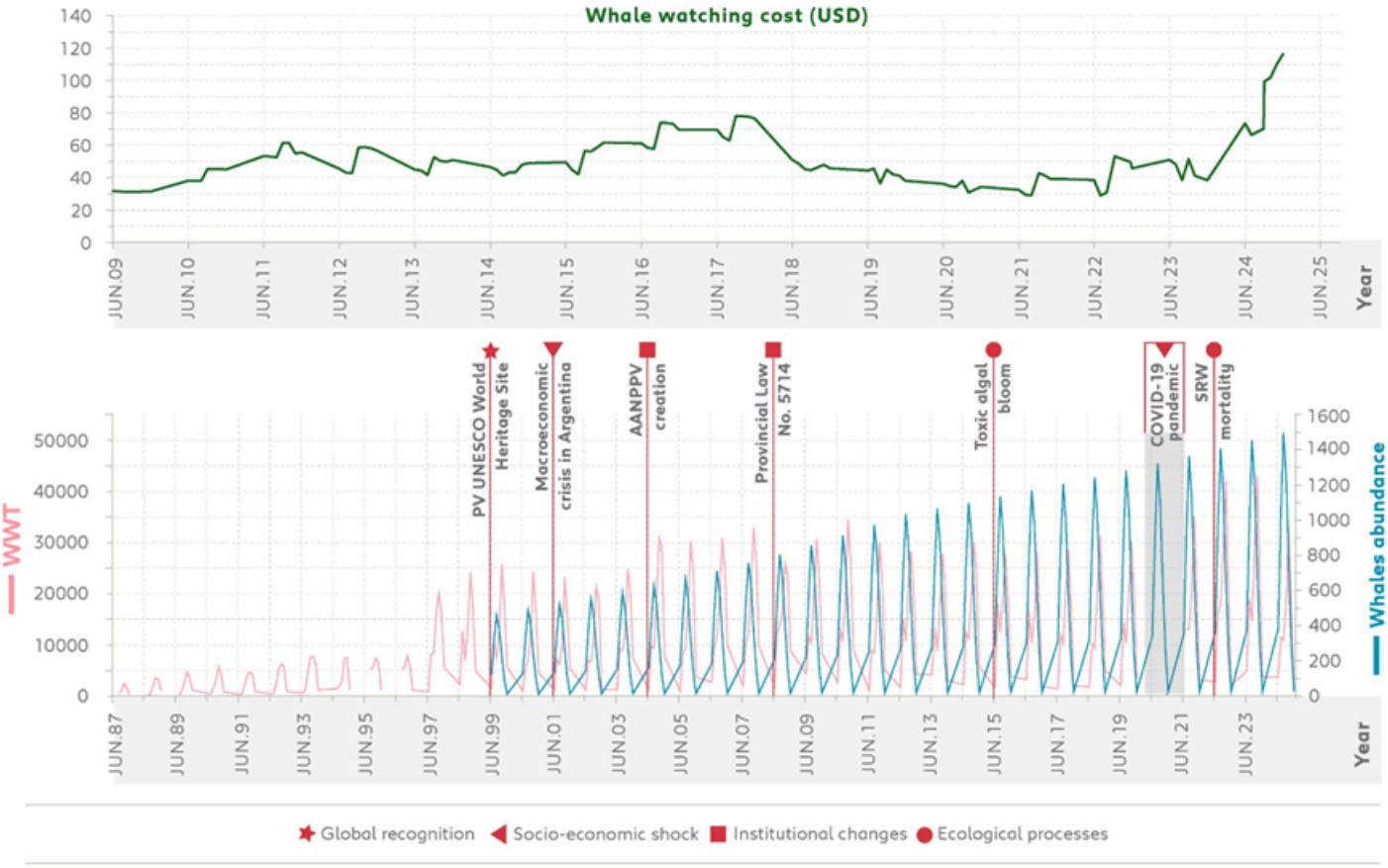


Figure 3

Decadal trajectories of the Península Valdés socio-ecological system (1987–2025). (Top) Evolution of whale-watching ticket costs in USD, reflecting the economic valuation of the service over time. (Bottom) Long-term synchronization between southern right whale (*Eubalaena australis*) abundance (blue) and tourism demand (WWT, orange). Markers denote key systemic shocks and institutional milestones, including UNESCO designation, provincial laws, macroeconomic crises, and ecological perturbations (toxic blooms and mortality events). This longitudinal record provides the empirical basis for the non-linear interaction testing (GAMs) discussed in Section 4.

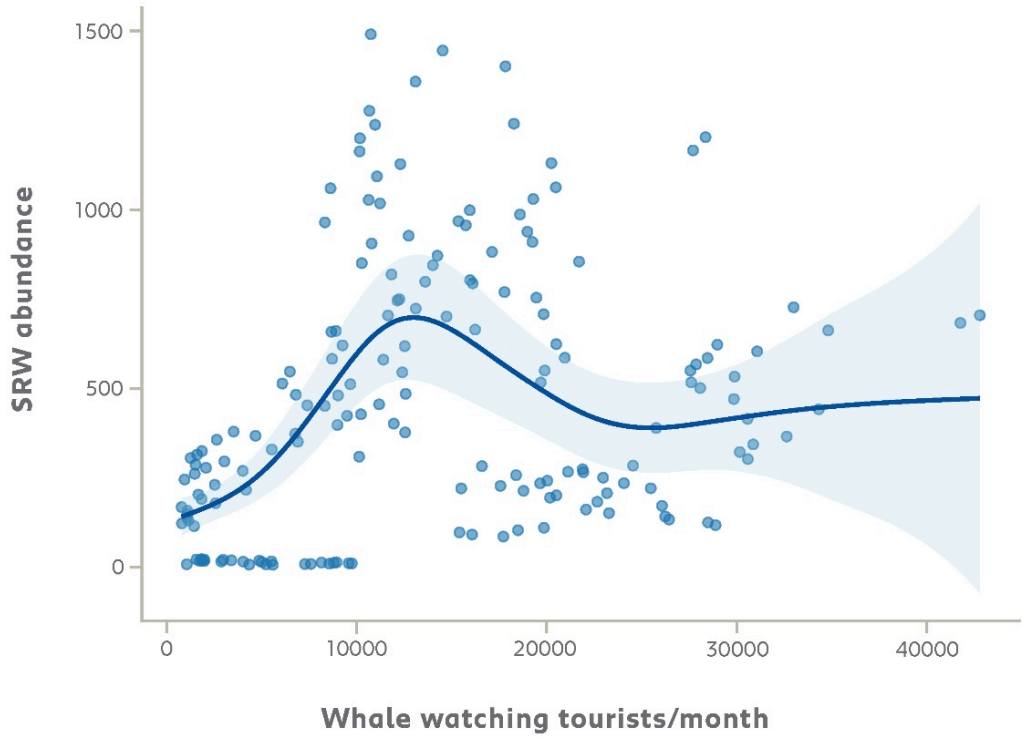


Figure 4

Nonlinear relationship between tourism pressure and whale abundance**.**
Generalized additive model (GAM) showing the relationship between the number of whale-watching tourists and Southern right whale abundance in Península Valdés. Points represent observed values, the solid line indicates the fitted smooth function, and the shaded area shows the 95% confidence interval. The nonlinear pattern suggests the presence of threshold dynamics and potential saturation effects in the socio-ecological system.

Supplementary Files

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- Supplementary.docx