Lessons from COVID-19 for wildlife ranching in a changing world

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The COVID-19 pandemic provided an opportunity to assess the impacts of a global disturbance on conservation land uses and learn from responses to the crisis to enable more resilient conservation systems. To understand socio-economic responses of diverse wildlife working lands to COVID-19, we surveyed owners and managers of 78 private wildlife ranches (wildlife working lands), 23 agricultural farms (conventional working lands) and six public protected areas (conventional conservation lands) in South Africa. Most protected areas lost more than 75% of their revenues during 2020, while most agricultural farms lost less than 10%. The impact on wildlife ranches was more varied. Ranches with more diverse activities, particularly mixed wildlife–agriculture systems, lost less revenue, shifting their activities from those heavily impacted (international ecotourism, trophy hunting) to those less affected (for example, wildlife meat, livestock). This adaptive capacity suggests that wildlife-based enterprises could represent key ecosystem-based adaptations, providing lessons for integrated global policies that seek to incorporate private land models in the 2030 Biodiversity Framework.

Curbing biodiversity loss requires transformative governance to strengthen the resilience of conservation strategies in a rapidly changing world[1,2]. Public protected areas remain the core global conservation strategy[3]. However, their effectiveness and ability to meet the proposed 2030 Global Biodiversity Framework target of 30% land conserved are impeded by limited resources (for example, skills, money and capacity), competing governmental interests and social justice trade-offs[4,5]. There is thus a need for additional conservation strategies, with increasing recognition of the role that private landholders and communities can play[6,7].

Private landholders and communities are involved in conservation through various models of working lands—lands managed both for production and ecological function[8]. Working lands include rangeland models such as silvopasture and holistic grazing management, which can contribute to food security, job creation and biodiversity

conservation simultaneously[8]. In Southern and Eastern Africa, private and community wildlife and mixed wildlife–agricultural ranches provide one such model. They enable innovative combinations of revenue-generating activities while also 'rewilding' habitats and increasing wildlife abundance[9–12], though these outcomes are contested in some contexts[13]. Assessing the ability of various wildlife working-land models to adapt to global shocks is key to designing policies that unlock resilient wildlife economies that benefit people and the planet.

Diverse models that support conservation (that is, protected areas, wildlife ranches, mixed farms) and tenure types (that is, state, private, community) can contribute diversity and redundancy in conserved ecosystems, resources, knowledge systems and management strategies[14–16]. Theory suggests there is a positive relationship between the diversity of elements in a system and its resilience[17], where

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resilience is defined as a system's ability to retain its identity (critical structures, functions and feedbacks) in the face of disturbance and change through self-organization, adaptation and learning[18]. In more diverse ecosystems, for example, it is less likely that a disturbance that causes species losses will cause the loss of entire ecosystem functions, due to diversity in species' responses to the disturbance[19]. Although this relationship is less well established in social–ecological systems, it is predicted that systems with diverse management models and institutions, for example, may be more effective at responding to change because diversity gives rise to higher levels of innovation, adaptation and resistance[16,20,21]. Diversity in actors and tenure types may therefore strengthen the resilience of conservation systems if it increases the ability to learn and adapt in response to disturbance and change (that is, adaptive capacity)[22].

Diversity in conservation actors can, however, also bring potential vulnerabilities: many community or privately conserved lands lack the institutional and financial safety nets afforded to public protected areas. Additionally, conservation in such lands is often an emergent outcome of enabling conditions (for example, policy and economic environments that make wildlife a competitive land use), rather than an objective in and of itself[7,10]. This raises questions about the ability of these working lands to continue contributing to conservation when conditions change, given their need to remain financially viable[21,23]. The COVID-19 pandemic was a major global shock that tested the resilience of conservation and other sustainable land-use systems around the world. The pandemic provided an opportunity to assess not only the impacts of a global disturbance on the economic sustainability of diverse conservation land uses but also to consider what we can learn from how these land uses adapted in the face of a crisis for enabling more resilient conservation strategies going forward.

Wildlife-based tourism in Africa generates US$29 billion annually (over one-third of all tourism to the region) and employs 3.6 million people[24]. The continent also attracts considerable foreign support for conservation via philanthropy and aid. The net conservation impacts of COVID-19 in Africa are believed to be strongly negative due to ailing economies and limited travel resulting in reduced funding and tourism revenues, restrictions on the operations of conservation agencies and elevated human threats to nature[25–28]. In South Africa, tourism revenue in national parks declined by 90% during lockdowns in 2020, resulting in a loss of community development revenues and educational programmes and cost curtailment measures to park management, such as ranger patrols[29]. These severe impacts bring into question the resilience of conservation models based primarily on managing for biodiversity conservation, which are dependent on revenue from ecotourism or external or state-subsidized funding[25,30,31].

Private wildlife and mixed wildlife–livestock ranches in South Africa provide a good opportunity to explore response strategies of working lands to a major shock and the relevance of the hypothesized relationship between social–ecological diversity, adaptive capacity and resilience. An estimated 14–17% of South Africa's area comprises wildlife-based land uses on private land[32]. Over 1,000 privately protected areas and 5,000 wildlife ranches play a central role in the country's conservation estate with demonstrated biodiversity conservation outcomes[9,16]. Their socio-economic contributions are also notable with wildlife ranches providing, on average, more jobs per hectare and higher-quality jobs than both agricultural farms[32] and public protected areas[33]. The hunting and ecotourism industries contribute millions of dollars to the national economy each year[32,34]. Some of these wildlife working lands have also been criticized, however, in cases where financial and conservation objectives are not aligned, leading, for example, to the persecution of predators to protect valuable species for trophy hunting or the stocking of high densities of charismatic megafauna in response to ecotourist preferences[13]. They are also owned predominantly by minority white South Africans and foreigners, reflecting inequities in land ownership that stem from the racially defined and discriminatory apartheid era that ended in 1994[35]. Several authors argue that the wildlife ranching industry has entrenched these inequities[36–38]. Understanding the response of wildlife working lands in South Africa to a major shock thus requires nuanced consideration of their contributions to conservation and socio-economic development, which could improve policy design that seeks to find equitable, sustainable solutions to biodiversity loss.

The proliferation of wildlife ranches over the past half century is largely due to policies that enable the use and ownership of wildlife on private land and lucrative non-consumptive (ecotourism) and consumptive (for example, hunting, meat and live-wildlife sale) industries that make wildlife a competitive land use[10,32]. Similar trends in the expansion of wildlife working lands and their socio-economic and conservation contributions are evident on community and private land in other Southern African countries[10,39]. These ranches are highly diverse in their motivations and business models (that is, the combinations of wildlife activities they undertake)[12,32,40]. The reliance of many ranches on (often international) visitors and the need to remain financially viable suggests that they may have been heavily impacted by the COVID-19 pandemic. While the estimated financial impact of COVID-19 on the private wildlife industry is severe[41], we hypothesize that the diversity of wildlife enterprises led to heterogeneity in impacts and responses to the crisis.

In this paper we consider if and how diverse South African wildlife ranches responded to the pandemic (Supplementary Fig. 1 provides a map of study sites). A clustering analysis of wildlife ranches based on their revenue-generating activities reveals four unique business models with two being more specialized (focused on ecotourism or trophy hunting) and two being more diversified (diverse wildlife activities or mixed wildlife and agricultural activities). We assess whether the business models adopted by wildlife ranches influenced the extent to which they were impacted financially by the pandemic, compared with agricultural farms (as an example of more conventional working lands) and public protected areas (an example of more conventional conservation lands). Importantly, we then assess the strategies that wildlife ranches implemented to cope with these impacts, highlighting the value of diverse business models for enhancing adaptive capacity. We consider potential implications of this adaptive capacity for the socio-economic and conservation contributions of wildlife ranches and conclude with lessons for building resilience in the wildlife and conservation sectors more broadly.

Results

During the 2020–2021 financial year, half of wildlife ranches lost more than 75% of their expected revenue and a quarter lost 50–75%, while 9% lost less than a quarter and 3% experienced an increase in revenue (Extended Data Fig. 1). Comparatively, nearly all public protected areas lost more than 75% of their expected revenue, and most agricultural farms lost less than 10% (Chi-square, X^2,-statistic = 57.83, degrees of freedom, df, = 1, $P < 0.001$; Extended Data Fig. 1).

On wildlife ranches, the most common revenue-generating activities were trophy hunting (sale of hunting experiences where the hunter, usually a foreign tourist, retains some of the animal's body as a trophy); wildlife breeding (sale of live animals with good genetics, usually to breed trophy animals); and ecotourism (sale of wildlife viewing experiences) (Fig. 1). Livestock farming (cattle, goats, sheep) was also undertaken on 41% of the properties with a smaller proportion of properties undertaking cultivation. On average, 66% (±4% standard error, SE) of visitors to these properties were foreign, though it varied from 0% to 100%. Of the landholders undertaking trophy hunting, 95% stated it to have been the activity most impacted by the pandemic, while 65% of landholders undertaking ecotourism stated it to have been the most impacted activity (Fig. 1). By contrast, less than 20% of landholders undertaking other wildlife-based activities (for example, biltong hunting, wildlife breeding, venison) stated that these activities were the most impacted
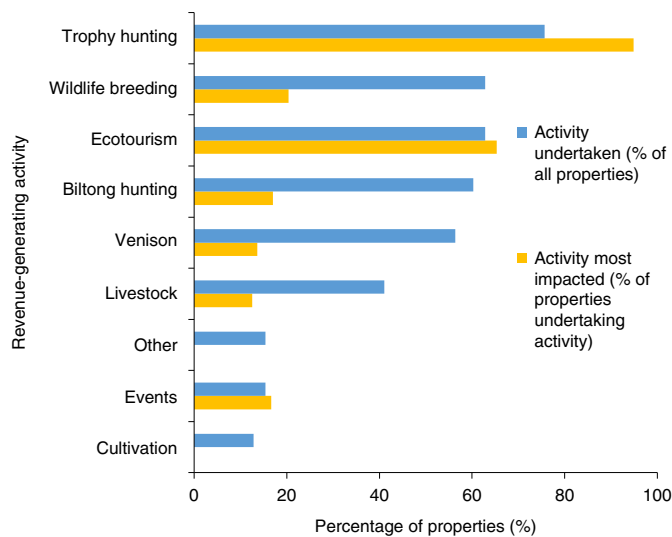
Fig. 1 | Wildlife ranch activities most impacted by the pandemic. Percentage of 78 wildlife ranches undertaking different revenue-generating activities and percentage of ranches undertaking a certain activity that reported it to have been most impacted by the pandemic.
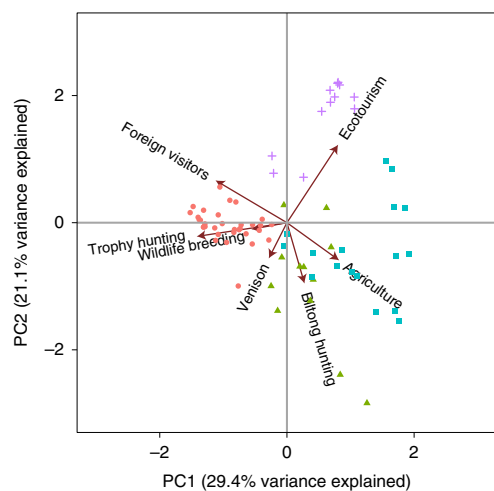
Fig. 2 | Biplot depicting trends in the contributions of different activities to wildlife ranch revenues, based on the relative scores of seven activities on two PCs. Data points indicate the PC scores of 74 ranches with shapes and colours corresponding to four distinct 'business model' clusters (pink circles: trophy hunting focus; green triangles: mixed wildlife; blue squares: mixed wildlife–agriculture; purple plus signs: ecotourism focus). Revenue losses during the pandemic were higher with lower values of PC1 (β-statistic = −1.00, standard deviation SD = 0.24, t-statistic = −4.15, $P < 0.001$) and higher values of PC2 (β = 0.74, SD = 0.24, t = 3.07, $P = 0.003$).

by the pandemic. Biltong hunting refers to hunting for meat, usually by South African hunters, and venison refers to the sale of wildlife meat.

The combination of revenue-generating activities adopted by wildlife ranches before the pandemic (represented by two principal components (PCs); Fig. 2 and Supplementary Table 1) predicted a quarter of the variation in the extent to which ranch revenues were impacted by the pandemic (R^2 = 0.253, F-statistic = 13.25, df = 2 and 70, $P < 0.001$). Two combinations of activities resulted in significantly larger revenue losses. The first was a higher proportion of foreign visitors and revenues from trophy hunting and wildlife breeding, combined with a lower proportion of revenues from ecotourism and agriculture (livestock

and/or cultivation) (depicted by the negative relationship between PC1 and revenue loss; Fig. 2). The second combination was a higher proportion of foreign visitors and revenues from ecotourism, combined with a lower proportion of revenues from biltong hunting, venison sales and agriculture (depicted by the positive relationship between PC2 and revenue loss; Fig. 2).

Four distinct clusters of wildlife ranches were evident, based on the combinations of revenue-generating activities that they adopted before the pandemic (Fig. 2; Mantel R = 0.56, n = 74). Trophy hunting-focused ranches (45% of properties) generated two-thirds of their revenues, on average, from predominantly foreign trophy hunters (Table 1). They undertook other wildlife-based activities and agriculture to a limited degree. By contrast, on mixed wildlife ranches (16% of properties), trophy hunting generated one-third of revenues, closely followed by biltong hunting, venison sales and ecotourism. These properties had majority South African visitors. Mixed wildlife–agriculture ranches (23% of properties) generated just over half of their revenues from agriculture (mostly livestock), with largely South African ecotourism making up one-fifth of revenues and other wildlife-based land uses comprising the remainder, on average. Finally, ecotourism-focused ranches (16% of properties) generated over 80% of their revenues from ecotourism, on average, focusing predominantly on foreign visitors. Other wildlife-based activities formed the remainder of their revenues, with almost no agriculture taking place, on average.

These four business models differed markedly in the extent to which their expected revenues were impacted by the pandemic (Fisher's $P < 0.001$; Fig. 3). The majority of trophy hunting- and ecotourism-focused properties lost >75% of their revenues. By contrast, many mixed wildlife–agriculture properties lost less than half of their revenues, with 12% actually increasing their revenues. Half of mixed wildlife properties lost between 50% and 75% of their revenues.

The most common coping strategy, adopted by 40% of landholders in response to the impacts of the pandemic, was to adapt their marketing strategies to attract local tourists and/or biltong hunters, often by offering discounted rates (Table 2). Over a quarter of landholders adapted by cutting down on operating costs—decreasing staff numbers or salaries, pausing new projects, for example. Just under one-fifth of landholders adapted by shifting their focus to livestock (and to a lesser extent cultivation), and a similar proportion shifted their focus to other wildlife-based activities beyond hunting and ecotourism, such as packaging and selling venison. Just over one-tenth of landholders mentioned their reliance on off-property income sources. Notably, 10% of landholders specifically mentioned supporting their staff to cope with the pandemic.

Wildlife ranches with different business models differed significantly in their strategies to cope with the pandemic (X^2 = 19.25, df = 9, $P = 0.02$; Fig. 4). All ecotourism-focused ranches reported cutting costs, and over half shifted their marketing focus to attract local tourists. No ecotourism-focused ranches shifted their focus to agriculture, and less than 10% focused on other wildlife-based activities beyond ecotourism. Just over 40% of trophy hunting ranches similarly cut costs and focused on local markets. In addition, over a quarter reported shifting their focus to agriculture and almost one-fifth focused on other wildlife-based activities. The most common strategy among mixed wildlife ranches was to focus on other wildlife-based activities beyond trophy hunting and ecotourism, particularly venison, and to focus on local markets. All four coping strategies were less common among mixed wildlife–agriculture ranches than the other three business models.

Discussion
Many wildlife-based working lands demonstrated adaptive capacity in the face of a major global shock. While the substantial impact of the pandemic on their revenues must not be overlooked[41], lessons can be learned from patterns in the degree to which different wildlife-based land uses were affected and the ways in which these enterprises responded to the crisis. Importantly, more diversified business models and mixed

Table 1 | Revenue-generating characteristics of wildlife ranches in four distinct 'business model' clusters (mean±SE)

	Trophy hunting focus (pink circles)	Mixed wildlife (green triangles)	Mixed wildlife–agriculture (blue squares)	Ecotourism focus (purple plus signs)
Number of properties	33	12	17	12
PC1	−0.52 (±0.21)	0.19 (±0.25)	0.65 (±0.37)	0.33 (±0.24)
PC2	−0.02 (±0.14)	−0.54 (±0.52)	−0.25 (±0.40)	1.00 (±0.31)
Revenue from (%)				
Ecotourism	4.9 (±7.1)	15.6 (±15.3)	21.2 (±28.3)	83.1 (±21.7)
Biltong hunting	5.3 (±5.4)	22.3 (±26.3)	6.1 (±6.9)	1.7 (±3.3)
Trophy hunting	65.9 (±16.8)	31.3 (±20.4)	9.4 (±12.4)	6.3 (±11.9)
Venison	6.4 (±8)	17.1 (±20.6)	1.8 (±4.3)	1.1 (±1.9)
Wildlife breeding	9.8 (±8.8)	4.3 (±6.6)	5.1 (±7.7)	5.5 (±6.5)
Agriculture (livestock and cultivation)	5.8 (±9)	2.8 (±6.9)	55.3 (±21.6)	0.5 (±1.4)
Livestock	5.3 (±9.1)	2.4 (±6.9)	50.9 (±24.3)	0.5 (±1.4)
Cultivation	0.5 (±1.9)	0.4 (±0.8)	4.4 (±10)	0 (±0)
Events	0.2 (±0.9)	1.8 (±5.7)	0.1 (±0.2)	1.4 (±3.1)
Other	1.8 (±7.1)	4.7 (±14.3)	1.2 (±3.8)	0.5 (±1.4)
Foreign visitors (%)	87.2 (±12.9)	29.6 (±21.4)	35.8 (±37.2)	85.2 (±12.5)

Colours and symbols refer to the respective clusters on Fig. 2.
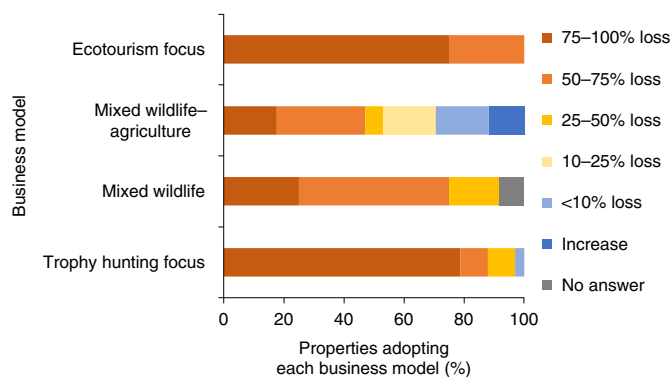
Fig. 3 | Impact of the pandemic on the revenues of wildlife ranches adopting different business models. Impact of the pandemic on expected revenues during the 2020–2021 financial year on 74 wildlife ranches adopting four business models.

wildlife–agriculture models were less impacted financially and better able to adapt by shifting revenue-generating strategies away from those worst hit, namely international ecotourism and trophy hunting. This supports the theory that diversity promotes adaptive capacity, an important aspect of resilience[17,20,22]. Adopting a specialized business model can cause path dependence through investment in specialized infrastructure, markets and capacities that constrain future options[42]. For example, specialized ecotourism areas were less able to adopt more consumptive wildlife activities, perhaps due to their prior investment into an international market that desires pristine, unutilized landscapes with high densities of charismatic megafauna[43,44]. Their high lodge start-up and running costs can also be a burden when revenues become limited[42].

The ability to adapt to maintain financial viability is critical for many wildlife working lands, yet some adaptations may not result in desirable socio-economic or ecological outcomes. For example, ecotourism-focused areas were more likely than wildlife consumption-orientated areas to adapt by cutting jobs in response to revenue losses. This has important implications for job security in rural areas and reveals that investment strategies focused on establishing

ecotourism ventures without incorporating the capacity to switch to other wildlife-economy revenue streams might undermine their long-term socio-economic contributions. Cost cutting in response to revenue losses may also undermine ecological outcomes if it results in diminished mitigation of threats to biodiversity such as invasive species or poaching[45]. The least financially impacted wildlife-economy model was mixed wildlife–agriculture areas, as many were able to adapt to the pandemic and some even increase their revenues. Notably, this model was able to adapt by scaling up less affected revenue-generating activities rather than cutting costs. Not all of these activities were wildlife-based however, and it will be important to monitor the long-term conservation implications of scaling up other farming activities (largely livestock and cultivation, which was less common but probably more impactful to conservation). While models based on international visitors (ecotourism and trophy hunting) can be lucrative activities in normal times[12,32,40], our results support the recommendation by Lindsey et al.[25] that building resilience requires diversifying the revenue streams from wildlife-friendly land uses to include domestic and international tourism, sustainable use and mixed land-use approaches.

The importance of multi-tenure conservation systems
More generally, our results speak to the importance of diversified conservation systems for promoting adaptive capacity (in this case, in the interest of retaining financial viability), which is probably important for strengthening the resilience of conservation efforts in a changing world. The private ranches in our study lacked the government support that allowed public protected areas to sustain their identity through the pandemic but because they were less institutionalized with fewer constraints on activities, many of these private areas also had the capacity to adapt their business models more easily. Although our public protected area sample size was small, these areas showed similarly high revenue losses during the pandemic to those reported across South African national parks by Smith et al.[29]. Conservancies in Botswana[26] and Zimbabwe[27] also experienced large losses because of over-reliance on a single income stream, but unlike South African national parks, were able to adapt and strategize beyond non-consumptive wildlife uses. Protected areas such as national parks are not only constrained by what the law requires them to do, but also by public perception and

Table 2 | Summary of key strategies adopted by 78 wildlife ranches to cope with the pandemic

Response	Details	Example quote from respondents	% of ranches
Focused on local markets	Shifted marketing to attract local visitors; advertised 'isolation' appeal; offered local discounts; shifted from trophy hunting to biltong hunting.	"Every farmer in the country is trying to get to the local hunters" "Local hunters really pulled us through" "They put out some South African specials to at least try and attract some local trade" "Lockdown (COVID-19) increased our revenue as more locals wanted to 'escape the city' and beaches were banned, so the mountains suddenly became very attractive"	40
Cut costs	Cut down on running costs; decreased staff salaries or time; retrenched staff; paused new projects; partially closed accommodations (closed some lodges or the enterprise over some weeks).	"That budget (to run land-management operations) alone was cut by 75%...just down to essential services—they (employees) can still make sure the fence is working, but they can't now go and attack alien invasive species" "We got rid of unnecessary vehicles, equipment, just kept what we could work around with" "We had to lay some staff off. We had to make some retrenchments or temporary retrenchments"	28
Focused on agriculture	Focused more on livestock farming, using farming income to fund the property; introduced cattle and/or goats; diversified into tobacco, flowers or nuts.	"I'm thankful that we diversified and made money out of the tobacco" "We increased cattle, goats and sheep to generate a second income" "We began farming with cattle and goats as soon as lockdown was announced"	17
Focused on other wildlife-based activities, beyond hunting or tourism	Venison processing, packaging and sale to local markets; moved to events or horse riding; undertook wildlife culling; increased live-wildlife sales.	"We moved to incorporate events and horseback safaris" "More biltong hunting and conferences. We also had to cull animals that would've been hunted and sold their meat on the local market"	17
Relied on other income	Funded costs through other income or savings, a loan or insurance.	"We coped by transferring some of our employees to other businesses and also relied on the income from some of our other businesses"	12
Supported staff	Avoided staff layoffs by applying for government support for salaries; provided food parcels or venison to staff; changed staff roles, for example, from visitor guides to anti-poaching or livestock.	"We were able to apply and receive UIF (Unemployment Insurance Fund) payments for staff, which enabled us to not permanently lose staff" "We cross-subsidized and used our income from cattle to fund the tourism staff"	10
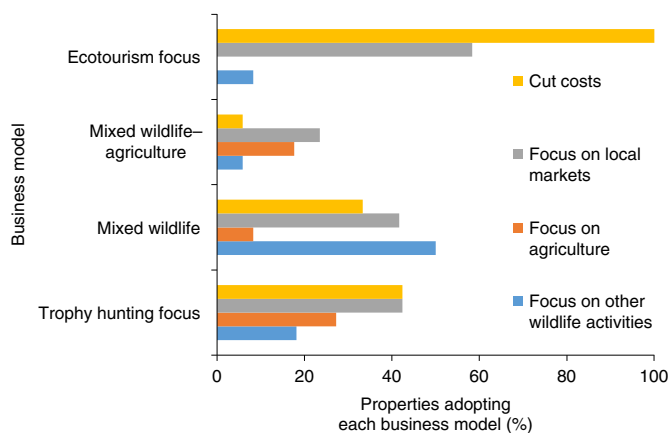
Fig. 4 | Reponses to the pandemic of wildlife ranches adopting different business models. Percentage of 74 wildlife ranches adopting four business models that reported adopting each of the most common responses to the pandemic.

values around how 'wild' and 'untouched' these areas need to be[29]. Whereas national parks are important for national identity, heritage and conservation[29,46,47], the need to manage them for optimizing a certain kind of biodiversity value can undermine economic sustainability[29]. Strict protected areas are often expensive for national treasuries and can therefore represent only a small fraction of a sufficiently comprehensive, diverse and resilient national conservation estate.

Beyond the COVID-19 pandemic, there are many more disturbances projected in the coming decades. Drought, wildlife, stock and crop disease, conflict over water rights, recessions, political instability, changes in agricultural subsidies, species range shifts and global preference changes could all have unpredictable impacts on the sustainability of individual protected areas and wildlife areas (for example, refs. [48–50]). Ensuring the resilience of healthy ecosystems to these disturbances requires conservation networks with sufficient response diversity in economic and governance models[16,51], supported by diverse values and motivations[1]. Such diverse systems will still experience conservation losses—in our study, over one-quarter of ranches cut operating costs (for example, anti-poaching and invasive species control efforts) in response to the pandemic, and some increased crops on their properties, possibly reducing biodiversity. The possible trade-offs associated with achieving economic sustainability for wildlife-based systems require consideration[6], recognizing that some trade-offs are inevitable under global change pressures. Enhancing the economic adaptive capacity of individual areas translates into a greater probability of maintaining wildlife-based land uses[3], which should support ecological resilience relative to counterfactual land uses such as cultivation. The nature of the relationship between economic and ecological sustainability on wildlife working lands, however, requires further attention and will depend partially on landholder motivations to manage for short-term profit over long-term land productivity and biodiversity and if trade-offs can be lessened by supportive policy.

Policy implications

Our results demonstrate that non-state actors on wildlife working lands are responsive to changing environments. Such adaptive capacity was similarly evident in the transition of private landholders and communities from livestock to wildlife in response to policy changes in southern African countries around the mid-twentieth century (including the introduction of wildlife property rights and the cessation of agricultural subsidies)[10] and in their diverse responses to the rhino poaching crisis[21]. It is important that policy is sufficiently flexible to allow for this adaptive capacity, while also seeking to incentivize the types of land use that are

desirable to countries as they navigate sustainable development. For example, governments could create enabling environments for more diverse land uses that include wildlife-based models to thrive, such as access to land and tenure security, avoiding over-regulation and increasing skills-development programmes for managing both wildlife and livestock simultaneously. These programmes should simultaneously emphasize sustainable land-management practices to ensure both wildlife and livestock production promote desirable ecological outcomes on these working lands[52].

As we have argued, and as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Global Assessment[53] emphasizes, strategies to curb global biodiversity loss require a mix of policies and funds that support a diversity of nature-positive economic and governance models, maintained by pluralistic values and motivations[1]. The 2030 Global Biodiversity Framework goals, in sentiment, support such a diverse portfolio of area-based strategies through, for example, the emphasis on other effective area-based conservation measures (OECMs)[7]. Many on the ground assessments for establishing OECMs (for example, Marnewick et al.[54]), however, still focus on protectionist ideas that favour single intrinsic values of nature as opposed to adaptive and financially viable working lands. In many countries, conservation agencies still favour, sometimes exclusively, policies that promote ecotourism enterprises akin to public protected area models (for example, South Africa's Biodiversity Stewardship programme, Conservation Covenants in Australia). Such approaches may inhibit the adaptive capacity of these areas, potentially undermining the resilience of national conservation systems. Similarly, policies that focus only on enhancing the economic or ecological sustainability of conservation-positive land uses without considering trade-offs for equity may not only undermine social justice but also the long-term resilience of these systems.

From a sustainable land-management perspective, the adaptive capacity of diverse wildlife-based working lands suggests they may be good models of ecosystem-based adaptations (the use of biodiversity and ecosystem services to adapt to life in a less predictable climate system[55]). As such, wildlife-based working lands should be a critical thematic focus of strategies and policies that seek to align integrated commitments under the three Rio Conventions in the Decade of Ecosystem Restoration. As wildlife-based working lands can also contribute substantially to sustainable development goals such as reducing hunger, poverty and providing employment[32], but also represent areas that may require societal transformation in ownership[36–38], they warrant strategic attention for policies seeking to achieve equitable integration of the Sustainable Development Goals.

Methods

Data collection

We developed a semi-structured questionnaire survey as part of the 'Sustainable Wildlife Economies Project' (https://www.wildeconomy.org) to assess the socio-economic, sustainable land-management and conservation contributions of South African wildlife ranches in comparison to agricultural farms and public protected areas. An initial survey was designed by the authors at a workshop in December 2020 and distributed to the private wildlife ranch associations for comments. A revised version was piloted at a workshop with members of Wildlife Ranching South Africa, a private wildlife ranching association with over 160 members in the Eastern Cape Province, and the survey revised according to stakeholder feedback. Of relevance to this study, the survey included questions on the proportion of visitors to the property that were foreign; the revenue-generating activities that were undertaken on the property before the pandemic and how much each activity contributed to total revenue; how severely total enterprise revenue for the 2020–2021 financial year was impacted by the pandemic relative to expected revenue; and which revenue-generating activities were most impacted. The survey asked wildlife ranchers what their key strategies were to cope with the effects of the pandemic. Survey

questions relevant to this study are included in Supplementary Material 2. Ethical clearance was obtained from Rhodes University (number 2021-2810-5892).

Twenty-three field assistants (recent graduates in environmental science-related disciplines) were hired to conduct the surveys in teams of two to four. These assistants were trained by experts in wildlife conservation and sustainable land management to conduct the survey. Training was conducted during a week-long workshop in February 2021, covering the scientific background of the project, social process-learning techniques, conflict resolution and survey testing and practice.

In collaboration with Wildlife Ranching South Africa and other private wildlife ranching associations, a media clip outlining the project and requesting expressions of interest to be surveyed was distributed through landholder networks estimated to reach at least 160 landholders. A project coordinator followed up with respondents to confirm dates for the survey, and field teams were assigned to each property. Working with local associations and networks helped to ensure that the diversity of business models was adequately sampled. A total of 113 surveys with consenting landholders or managers in the Eastern Cape Province of South Africa were conducted in person between February and March 2021. Most respondents (>80%) were male and middle-aged (40–60 years). Three-quarters of these areas (82) were privately owned wildlife ranches (that is, >10% of the enterprise's revenue was generated from wildlife-based activities), 24 were private agricultural farms and seven were public protected areas. Mixed farms (that included wildlife-based and livestock activities) were thus largely classified as wildlife ranches. We included agricultural farms (working lands that probably generally experienced less impact from the COVID-19 pandemic because they are not reliant on tourism or hunting) and public protected areas (the standard for area-based conservation), as reference states. Surveys lasted between two and four hours. Respondents were made aware of the goals of the project, that all questions were optional and were assured of anonymity. No financial or in-kind compensation was provided. Data were captured by a scribe in hard copy during the survey and later entered into the Open Data Kit (https://opendatakit.org/) application, which allows for structured, distributed mobile data collection[56].

Data analysis

Five private properties and one public protected area were excluded because they provided insufficient information. We assessed the extent to which 78 wildlife ranches, 23 agricultural farms and six public protected areas were impacted by the pandemic based on a categorical score of revenue loss or gain over the 2020–2021 financial year (March 2020 to February 2021; Supplementary Material 2). We further assessed which revenue-generating activities on wildlife ranches were most impacted, relative to the percentage of landholders undertaking each activity. If landholders listed more than one activity as most impacted (for example, trophy hunting and ecotourism), we counted both in the analysis.

To assess whether the combination of revenue-generating activities on a wildlife ranch influenced the extent to which expected 2020–2021 revenue was impacted by the pandemic, we performed a principal component analysis (R package: vegan; function: 'rda') followed by a hierarchical agglomerative cluster analysis. We included 74 wildlife ranches for which we had complete data on revenue-generating characteristics. Characteristics included the proportion of revenue generated on the property from the six most common activities: trophy hunting, wildlife breeding and live sales, ecotourism, biltong ('meat') hunting, venison (meat) sales and agriculture (livestock and/or cultivation) and the proportion of visitors to the property that were foreign. The six revenue-impact categories were recategorized on an ordinal score from 1 (increase in revenue) to 6 (75% to 100% of revenue lost). We assessed the extent to which the two principal components representing combinations of revenue-generating activities explained variation in the degree of revenue loss using a linear model.

Distinct business models (that is, combinations of revenue-generating activities adopted by wildlife ranches) were identified using a cluster analysis, which employed Euclidean distance and Ward linkages (R packages: vegan and stats; functions: 'vegdist' and 'hclust')[57,58]. We used a Mantel-based comparison to identify the number of distinct clusters (R package: cluster; function: 'daisy')[59]. Differences between the business models identified by the cluster analysis were described according to the mean values of revenue-generating characteristics within each group. We then compared between business models the frequency of reported revenue losses/gains across categories using a two-sided Fisher's exact test.

Landholder responses to the question 'What were your key strategies to cope with the effects of the pandemic?' were categorized into broad themes on an iterative basis based on critical reading of all surveys. We assessed how many landholders reported each strategy (strategies adopted by 10% or more of landholders are included in the results) and compared the frequency of four most common strategies across business models using a two-sided Chi-squared test. Statistical analyses were performed in R[60] at a significance level of $\alpha = 0.05$.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All figures and tables in this study (both in the main text and supplementary material) relate to the dataset collected via surveys, as described in the methods. As we are bound by ethical considerations of the sensitivity of the data and committed to honour the trust placed in us by respondents to keep their data confidential, we cannot post the dataset publicly. We are, however, similarly committed to transparent and open science, and anonymized data with all identifying details removed can be requested from the corresponding authors for the purpose of validating our results independently, on the condition of signing a non-disclosure agreement.

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Author contributions

H.S.C. led the manuscript and performed most analyses. H.S.C., A.D.V. and M.F.C. contributed most of the writing of the original manuscript draft. A.D.V. led initial submission of the manuscript and contributed to the analyses. All authors contributed to conceptualization, design, framing, data collection and providing critical conceptual input.

Competing interests

The authors declare no competing interests.

Additional information

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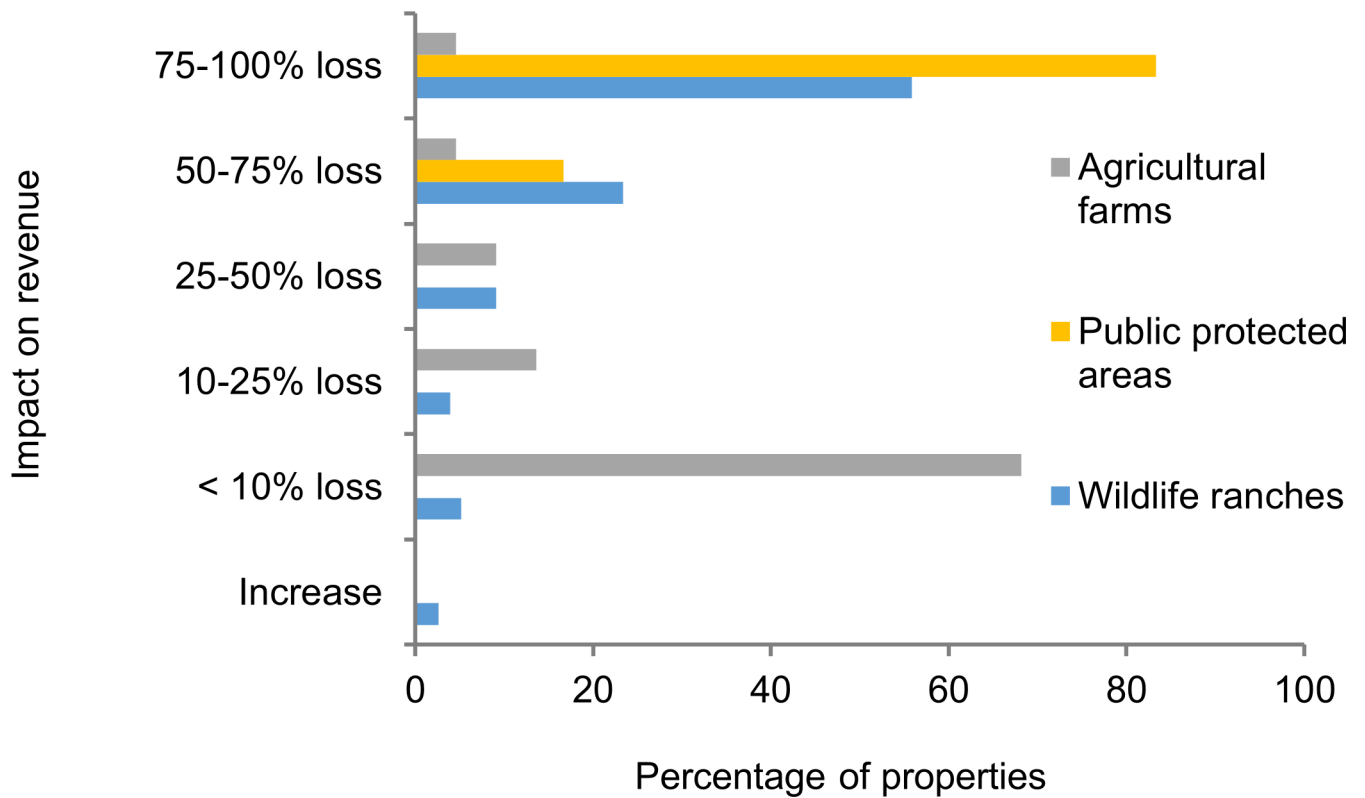**Extended Data Fig. 1 | Impact of Pandemic on Revenue.** Impact of the pandemic on expected revenues during the 2020/21 financial year, for 78 wildlife ranches, 6 public protected areas (PAs), and 23 agricultural farms.

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Software and code

Policy information about availability of computer code

Data collection	Open Data Kit (v1.25, 2019) were used to collect data, with data initially stored in a access-restricted Google Sheet. Collected data were downloaded and cleaned in Microsoft Excel (version 2011) and R project for statistical computing (v 4.0.5)
Data analysis	Collected data were downloaded and cleaned in Microsoft Excel (version 2011) and R project for statistical computing (v 4.0.5). We used R package: vegan; function: rda to perform a principal component analysis. We used Euclidean distance and Ward linkages (R packages: vegan and stats; functions: vegdist and hclust) to perform a cluster analysis, and used the R package: cluster; functions: daisy and silhouette to perform a Mantel-based comparison to identify distinct clusters. Code used were standard code associated with these packages and functions.

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All figures and tables in this study (both in the main text and supplementary material) relate to the dataset collected via surveys, as described in the methods. As we are bound by ethical considerations of the sensitivity of the data and committed to honour the trust placed in us by respondents to keep their data confidential, we cannot post the dataset publicly. We are, however, similarly committed to transparent and open science, and anonymised data with all identifying details

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Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We developed a semi-structured questionnaire survey to assess the socio-economic, sustainable land management and conservation contributions of South African wildlife ranches, in comparison to agricultural farms and public protected areas. An initial survey was designed by the authors at a workshop in December 2020. This semi-structured schedule was workshopped with stakeholders, and trialed, and then revised before data collection commenced.
Research sample	We interviewed 112 owners and managers of wildlife ranches, protected areas and agricultural farms. These individuals were largely male and middle-aged (we did not specifically collect demographic information). Three-quarters of these areas (82) were private wildlife ranch owners or managers, 24 were private agricultural farm owners or managers, and seven were public protected area managers. The focus of the survey was on private wildlife ranches, hence we collected more samples of these sites. We aimed to get as high as possible a sample size given the time and resources available. No compensation were offered to participants.
Sampling strategy	We largely employed convenience sampling, due to the difficulty of recruiting private wildlife managers and owners of interviewees. We worked with a local (national) wildlife ranching association, who contacted members on our behalf for voluntary recruitment. This association has the widest diversity of members of such associations in the country, which allowed us to get a more representative sample. A project coordinator followed up on these voluntary leads and organized the interviews. We also employed snowball sampling to find additional properties.
Data collection	Twenty-three field assistants (recent graduates in Environmental Science-related disciplines) were hired to conduct the interviews in teams of two to four. These assistants were trained by experts in wildlife conservation and sustainable land management to conduct the survey. Training was conducted during a week-long workshop in February 2021, covering the scientific background of the project, social process learning techniques, conflict resolution and survey testing and practice. Data were collected on hard-copy maps and paper initially. Teams reflected on, and discussed, their collected data and submitted cleaned data via the Open Data Kit Mobile Data Collection application to a central depository. Data were cleaned by the authors and a data assistant.
Timing	February and March 2021
Data exclusions	Five private properties and one state-owned area were excluded because they provided insufficient information for the purposes of this analysis.
Non-participation	An estimated 40-50% of contacted interviewees declined to participate, mostly on account of mistrust of researchers and the government, or lack of time. None of the participants that agreed to the interview withdrew from the interviews.
Randomization	NA

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☒	☐ ChIP-seq
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Human research participants

Policy information about studies involving human research participants

Population characteristics	See above
Recruitment	As explained in the "sampling strategy". Although Wildlife Ranching South Africa is the biggest ranching association in South Africa, they are not the only one, and more strongly represent local compared to International owners. It is thus possible that foreign owners and owners who do not belong to an association and are less connected, are not as well represented in our sample. The business models represented in our study match activities identified in the broader literature for South African ranches, so the latter is less of a concern, but it is possible that foreign owners have different coping strategies to local owners, and that the prevalence of some of these coping strategies may be under-represented in the results (they are, however, not absent).
Ethics oversight	Rhodes University Ethics Research Committee , no. 2021-2810-5892. (Chairperson at the time: Prof. Arthur Webb, a.webb@ru.ac.za, Current chairperson: Dr. Janet Hayward, Janet.Hayward@ru.ac.za).

Note that full information on the approval of the study protocol must also be provided in the manuscript.